# ECOLOGY AND PHYSIOLOGY OF THE RED MANGROVE.

(Plates IV–IX.)

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## General Statement.

When the plan for the pursuit of these studies was considered in the winter of 1914, the main idea was to make an effort to learn a little about the physiology of these interesting viviparous plants. Especially was it the aim to study the transpiration and absorption relations of these trees growing in salt water. Accordingly the splendid resources of the Carnegie Institution of Washington were offered and in June of 1915 the work was begun at the Institution's Marine Laboratory located in the Dry Tortugas.

During the first summer considerable ecologic observation was made during a month's stay at Key West, Florida, the institution having furnished the investigator with a launch and two men. Many observations were taken on the growth habits of the plants, the character of the bottoms on which they grew, the depth relations, tidal effects, the flowering and fruiting conditions, growth rates of hypocotyls and of aërating roots, water densities, dimensions of roots and aërial structures, heights of trees and general distribution about Key West and adjacent islands.

In July, after going to Miami and thence down through the Florida Keys on board the institution's yacht, *Anton Dohrn,* and notes on the mangrove being taken at various keys on the trip, the real laboratory work was commenced at the Tortugas. During the six weeks' season of the laboratory, several trips were made up to the Florida Keys for suitable plants and also for material on which to work during the winter. At this time it was determined to enlarge the scope of the work and to study some of the anatomical and histological features of *Rhizophora mangle,* and with this end in view material was carefully collected of all parts of the plants and preserved for future study. Meanwhile, the transpiration work was pursued and some attempt made to correlate the structure of special organs with the physiological functions in these plants which grow in such peculiar conditions.

In the winter of 1915–16 the study of these structures was carried on at the botanical laboratory of the University of Pennsylvania and again in June, 1916, a full season was spent at the Tortugas Laboratory on the physiology and also the biochemical relations of certain products in the hypocotyls. Short reports of the two summers' work were published in the year books of the Carnegie Institution.[1]

While considerable work has been done on the mangroves of the tropics in general, this has been mostly of a purely morphological nature, or ecological. The mangroves of our own tropical coasts have not been given as much attention as these plants might deserve; while the physiological relations have only in a few notable instances been made the subject of detailed study. The most extensive work has perhaps been done at the Buitenzorg Botanical Garden in Java by Haberlandt, etc.

In South Florida, although the climate is not like that of Java, the facilities afforded for study of mangroves is fairly good, but a great handicap has been found in the pursuit of this research, viz., that owing to the character of the soil and other considerations there are no mangroves in the Dry Tortugas and all the material had to be brought from the Lower Florida Keys with a consequent loss of many seedlings. Other studies which would have been made, particularly on the embryology of *Rhizophora,* have been deferred for the present until a tropical laboratory can be secured, where the plants can be secured conveniently, quickly and in abundance.

During the summer season of 1916 fortune favored the work at Tortugas in as much as seedlings were found in considerable quantity on the beaches of the islands composing the group. These viviparous seedlings had been drifted westward from the Marquesas

[1] Bowman, H. H. M., *Carnegie Institution Year Books,* 1915, p. 200; 1916, pp. 188–192.

and other islands by the current during the early spring season of higher tides and, on being washed ashore, took root to eke out a precarious and mostly fleeting existence.

Almost the entire first half of the season of 1916 was devoted to the biochemical research mentioned above. This work of testing for various chemical substances in the hypocotyl or storage organ of the seedling and the attempt at detecting enzymes in the organ could most conveniently be pursued at this time. During the interval which occurred from the time, in the early part of the season, when the young plants needed for the transpiration work were gathered and planted in the culture jars until they became established in their laboratory condition, the chemical work was carried on. Only after the plants had recovered from the shock of transplanting and were reacting normally to their changed environment was it deemed advisable to begin the transpiration work.

At the close of the 1916 laboratory season in August, the investigator accompanied the officers and crew of the yacht on her return trip north through the Florida Keys to be placed in winter quarters at Miami. On this journey of several days' duration, many distribution notes were taken and maps made of the keys and the absence of *Rhizophora* on certain keys carefully marked.

After the yacht had been moored up to her dock in the Miami River and shrouded in canvas for the winter, eight days were spent making observations on Biscayne Bay, the Miami River and Arch Creek on the admirable newly constructed launch possessed by the institution, the *Darwin*. These observations were made with the assistance of the yacht's chief engineer, Mr. John Mills, whose skillful operation of the launch, often in shallow and difficult channels, and whose help with the instruments was much appreciated. Tests by the hydrometer were made on the density of the water, both top and bottom layers, from the open Atlantic, across Biscayne Bay and up the Miami River and Arch Creek as far as any mangroves extended. Material was gathered for later study of both salt and fresh water trees and numerous transpiration records were taken on the pneumatophore prop roots of the mangrove under conditions and environments difficult for growth.

In conclusion of this statement the writer wishes to acknowledge the valuable aid given him by Professor J. W. Harshberger, whose wide experience in plant ecology and helpful guidance in the preparation of this paper have been of great assistance, especially on the geographic and ecologic aspects of the work. The author's thanks are also due the colleagues of Professor Harshberger in the University of Pennsylvania for their very kind help and suggestions, to Dr. J. Hepburn, of the U. S. Food Research Laboratory, for his expert advice in regard to enzymes, to Mr. Robert E. Dengler, Fellow in Greek, for his assistance in translating the classic and Renaissance references, to Mr. W. R. Taylor for aid in making the illustrations, to Dr. A. G. Mayer, of the Carnegie Institution of Washington, for many helpful suggestions, and to Engineer John Mills, and Captain L. M. Wilson, of the Tortugas Laboratory for their patience, consideration and excellent practical aid rendered on many field excursions in the Gulf.

## History.

The historical references to the subject of these studies are quite varied and reach far back into antiquity. Just as perhaps all science may be traced back to the Greeks, so in this instance we can turn to them for some early knowledge of the existence and peculiar habits of this plant, the *Rhizophora mangle.*

The earliest reference in ancient manuscripts is contained in the chronicle of Nearchus (325 B.C.). This old Greek sea-captain was the commander of Alexander the Great's fleet and fragments of his observations have come down to the present through the writings of Arrian. Nearchus sailed from the Indus Delta on the 21st of September, 325 B.C., and arrived in Susa, Persia, February, 324 B.C., shortly after Alexander himself had reached there by marching overland.

On this jounrney Nearchus[2] describes the habitat of the mangroves. Whether these trees are the *Avicennia* or *Rhizophora mucronata,* both of which grow in the region traversed by Nearchus, is not quite certain, but, by the description of the species in Theophrastus[3] and in the light of Bretzl's[4] recent work, in which the

[2] Nearchus, "Arr Anab.," VI., 6, 7.

[3] Theophrastus, "Historia Plantarum," IV., 7, 4–7.

[4] Bretzl, H., *Botanische Forschungen des Alexanderzuges,* 1903.

present species of the Red Sea, the Persian Gulf and the Indus Delta have been compared with those mentioned in the classics as noted on Alexander's March, there is now little doubt that the *Rhizophora* has been accurately described by these early mariners.

Theophrastus, 305 B.C.,[5] the pupil and successor of Aristotle, in his "Historia Plantarum" quotes Aristobulus as having seen in "the desert Gedrosia, trees that are about 30 cubits tall and have a flower that looks like a white violet and has a far-reaching odor." Nearchus also noted the relation of the plants to the tides, for he is quoted as observing them in Sec. 4, ἐν δὲ ταῖς νήσοις ταῖς ὑπὸ τῆς πλημυρίδος καταλαμβανομέναις, *i. e.*, in the islands which are reached by the flood tide, and also in Sec. 5 (καθ' ὃ ἡ πλημυρὶς γίνεται δένδρα ἐστίν) he says: "Wherever the floodtide reaches, there are these trees."

However, in Sec. 4, 7, Theophrastus gives the fullest description of the *Rhizophora*, "ἔχειν δὲ τὸ δένδρον φύλλον μὲν ὅμοιον τῇ δάφνῃ, ἄνθος δὲ τοῖς ἴοις, etc.," and the tree has a leaf like a laurel, but a flower like a violet both in color and odor, and a fruit the size of an olive, and this fruit is also fragrant. It does not cast its leaves, but the flower and the fruit both appear in the fall and they drop off the fruit in the spring." Bretzl thinks that the Greeks on account of being with Nearchus at the Indus Delta in September and in the Persian Gulf in February were in a position to be acquainted with both these phenomena. The mention of a violet-like odor is persistent not only in these early Greek writings, but also in the works of much later botanists, even down to the eighteenth century.

Theophrastus admirably describes the habit of the mangrove in growing out in rather deep water, where he says in Sec. 5: "These trees are all washed by the sea up to their middle," and in Sec. 4 "and they are held up by their roots like a polyp, for whenever there is an ebb-tide these (the roots) may be seen." He describes the pneumatophore prop roots of the *Rhizophora*, and again he says: "Some have their roots always flooded by the sea as many as grow in hollow places whence the water does not flow away and nevertheless the tree does not perish at the hand of the sea." Theophrastus also reports the ecological relations of the *Rhizophora* and

[5] Theophrastus, "Historia Plantarum," IX., 4, 2.

explains its xerophytic structure as due to the physiological dryness of its habitat: δηλοῖ δὲ ἡ στενοφυλλιά . . . , πάντα γὰρ ταῦτα ξηρότητος, "it is clear the narrowness of the leaf is due to the dryness."

Besides the many fragmentary references in Theophrastus to the mangrove, similar to those given above, he gives a very complete picture in Sec. 4, 7, 5, where, after mentioning the evergreen appearance of the trees and the times of fruiting and flowering, he says: "and there are other trees growing in the sea, evergreens, and they have fruit like beans and about the Persian Gulf, in the part toward Karmania, as far as the flood tide reaches, there are trees of quite some size, with leaves shaped like purslane, and it has a fruit much like an almond in color on the outside, but it is rolled together as if it were contracted; and these trees are all watered up to their middle by the sea and are held up by their roots like a polyp. For whenever there is an ebb tide these can be seen and the water is not wholly in this place and there are left certain channels through which they (the natives) sail, these are of sea water from which it is clear as some think, that they (the trees) are nourished by it and not by fresh water unless some is drawn by the roots from the earth, and that salt water is beneficial for them, for the roots go to no great depths."

This description might describe the mangrove thickets and swamps of the Florida Keys just as accurately as it fits those of the Persian Gulf and shows how observant were these early Greeks. Not only is it accurate as to general description, but Bretzl has been able to locate the actual stations for present species by these descriptions in Alexander's march.

Pliny the Elder (77 A.D.)[6] in his "Natural History," XII., IX.,[20] "Gentis supra dictas Persis attinget . . . intus contortis nucleis," does not contribute anything to the account of the Alexandrine companions and the above passage shows the influence of Theophrastus (325 B.C.) even to the very phrases. "Adjoining the countries which we have previously mentioned is Persis, lying along the shores of the Red Sea, which, when describing it, we have mentioned as the Persian Sea, the tides of which penetrate far into the land. The trees in these regions are of a marvelous nature, for,

[6] Pliny, S. C., "Nat. Hist.," XII., IX., 20 (37), Bohn trans., III., p. 117.

corroded by the action of the salt, and bearing a considerable resemblance to vegetable substances that have been thrown up and abandoned by the tides, they are seen to embrace the arid sands of the seashore with their naked roots just like so many polypi. When the tide rises, buffeted by the waves, there they stand, fixed and immovable, nay, more, at high water they are completely covered, a fact which proves to conviction that they derive their nutriment from the salt contained in the water. The size of the trees is quite marvelous; in appearance they strongly resemble the arbute; the fruit which on the outside is very similar to the almond, has a spiral kernel within."

In 70 A.D. Plutarch[7] published his "Moralia" and under the heading of **ΑΙΤΙΑ ΦΥΣΙΚΑ**, Nature studies, discussed the topic or question *Διὰ τί τὸ θαλάττιον ὕδωρ οὐ τρέφει τὰ δένδρα;* or "What is the reason that seawater nourishes not trees?" The passage is given in full, as the argument is sustained very quaintly throughout the paragraph. "Is it not for the same reason that it nourishes not earthly animals? For Plato, Anaxagorus and Democritus think plants are earthly animals. Nor, though sea water be aliment to marine plants, as it is to fishes, will it therefore nourish earthly plants, since it can neither penetrate the roots, because of its grossness, nor ascend, by reason of its weight, for this among many other things, shows sea water to be heavy and terrane, because it more easily bears up ships and swimmers. Or is it because drought is a great enemy to trees? For sea water is of a drying faculty; upon which account salt resists putrefaction, and the bodies of such as wash in the sea are presently dry and rough. Or is it because oil is destructive to earthly plants and kills things anointed with it? But sea water participates of much fatness; for it burns together with it. Wherefore, when men would quench fire we forbid them to throw on sea water. Or is it because sea water is not fit to drink and bitter (as Aristotle says) through a mixture of burnt earth? For a lye is made by the falling of ashes into sweet water, and the dissolution ejects what was good and potable, as in men, fevers convert humors into bile as for what woods and plants, men talk of growing in the Red Sea, they bear no fruit but are nourished by rivers casting up

[7] Plutarch, "Moralia," 911 *D–F*, Goodwin trans., III., p. 495.

much mud, therefore they grow not at any great distance from land but very near to it."

In the paragraph in which he has discussed the qualities of sea water and the difficulties of its utilization in the plant economy Plutarch almost suggests the theories of absorption and the ionization of solutions. The occurrence of the "woods and plants" in the Red Sea is also mentioned at another place in the "Moralia."[8] "And the provinces of Gedrosia and Troglodytes, which lie near the ocean sea, being by reason of drought barren and without any trees, there grow, nevertheless, in the adjacent sea, trees of a wonderful height and bigness, and green even to the very bottom, some of which they call olive trees, others laurels, and others the hair of Isis. And those plants which are named anacampserotes being hanged up after they are plucked out of the ground not only live but—which is more—bud and put forth green leaves."

The influence of Nearchus and Theophrastus is seen in the reference to the olive and laurel but the "anacampserotes" are not mentioned in the earlier authors. The word meant "bringing back love" and the plants were used in making love philters. The plants are, from the description, evidently the seedlings of *Rhizophora* which have just been rooted, but whether the ancients really regarded those seedlings as having an aphrodisiacal effect can not be accurately determined.

Arrian, 136 A.D.,[9] is the last of the classic writers to mention the mangrove. In his "Anabasis" he quotes Aristobulus and Nearchus in describing the plants observed on Alexander's march through Asia, but the references are essentially all alike and perhaps Theophrastus in his "Historia Plantarum" summarized all the observations on *Rhizophora* of his day and all the later authors copied the accounts as reported by Alexander's companions. There are not any mangrove references then in literature from Arrian's time, 136 A.D., until almost the middle of the thirteenth century.

In 1230 the Moorish botanist, Abou'l Abbas en-Nebaty,[10] after exploring Spain, Barbary coasts and Egypt made a long expedition

[8] Plutarch, "Moralia," ed. Bernardakis, 5, 455, Goodwin, V., 278.

[9] Arrian, "Anab.," VI., 22, 4 f.

[10] Abou'l Abbas en-Nebaty, Introd. to "Ibu el-Beithar" (Leclerq), V. Notices des Manuscrits, T. 23.

into Arabia, Syria and Irak. On his return to Spain he published his work, "Al Rihla," "The Journey," and died at Seville in 1239. This book, "Al Rihla," is not extant, but Abou's disciple, Ibn el-Beithar, has preserved citations from the book, as well as other Moorish writers, Ibn Hassan and Abou Hanifa. The references to the *Rhizophora* are very clear and it is due to these Moors that the mangrove was given the name *kendela*, which is an Arabic word. Both Abou Hanifa and Ibn Hassan describe the plant *kendela* and the former says[11] that "The water of the sea is injurious to every species of wood except the *quorm* (*Avicennia*) and the *kendela* (*Rhizophora*)," and under species "1981 kendala" he says: "It is a plant which grows in the country of the Deibol (on the sea of Oman) and which spring up in the sea. In that country it is employed in the tanning of hides, known under the name of leather of Deibol, which is red and thick. It furnishes also a red bark which is used as part of medicaments for the mouth and of those which are used to stop hemorrhages."

The name *kendela* was later spelled *candela* or *kandila* by the sixteenth and seventeenth century botanists and applied to the mangrove on account of the resemblance of the prolonged hypocotyl, as it hangs on the tree, to candles.

From 1230 to 1526 is another long gap in the literature on the mangrove. About this latter year Oviedo[12] put forth his book dealing with his travels in the Indies. The observations of this early Spanish explorer and those of his successor give us the first glimpse of the vegetation of the western hemisphere from a purely botanical standpoint. Later botanists quote Oviedo and Clusius[13] (1584) and Peter Martyr[14] (1577) and several particularly mention Oviedo's experience with the fruit of *Rhizophora*. "I nevertheless," he says, "from its use (as food) fell into sickness although I am not so delicate nor accustomed in time of want to abstain from those foods which I see others eat, but neverthless, although there was no

[11] Abou Hanifa, "Ibu el-Beithar," Leclerq. Notices des Manuscrits, T. 23, 25, 26.

[12] Oviedo, G. F., "Primera Parte de la Historia Natural general de las Indias," 1526.

[13] Clusius, Carolus, "Rariorum Plantarum Historia," 1601.

[14] Martyr, Peter, "Edens. History of Travel," 88, 143, 1577.

urgent necessity it did not offend me to taste it, so that I might describe it the more accurately, and so for that reason I tasted the fruit but it seems that it should be called rather, the food of brute animals and wild men of the woods." From the writings of Clusius and Oviedo thus it seems that the natives of the West Indies used the hypocotyl as a source of food in famine times, probably on account of the starch they contain, but as Piso says they must have had a special method of preparing them to eliminate some of the tannin.

In 1648 Piso[15] and Marcgraf noted the mangrove as it occurred along the shores of Brazil. Under the chapter heading "Devariis specibus Mangues, sive Mangles et earum qualitatibus," Piso describes their habitat as "in swampy places by the sea in the Indies and all the tropics." He quotes Clusius and also says there are three species of mangles. "Prima, *Cereiba,* quæ Mangue est alba; Secunda *Cereibuna,* quæ non radices ex ramis in terram agit, nec tam tortuoso plexu luxuriat." And the third, which is our *R. mangle,* is called *Mangue Guaparaiba.* It is, according to the account, of larger size than the two preceding species and bears useless pods in the summer months, which are filled with bitter pulp.

In 1650 Bauhin[16] in his "Universal History of Plants" quotes Oviedo and Lobez in giving a description of the tree and says: "F. L. (Lobez) mentions a certain tree growing in the province of Malay which they call 'Mangin,' bearing roots above, like stems," Clusius questions whether this be our Indian fig but we (Bauhin) put the mangin or mangle because of the closeness of the name to mangle, with which tree it also seems to correspond, as Ferdinand Lobez describes it." Du Tertre, 1667,[17] mentions the mangrove and Rochfort, 1681,[18] in the book of travels in the Antilles describes the tree, called paratuvier, and its rooting habits, and says: "Wild boars and other savage beasts live in them, and they afford places of shelter for the inhabitants, who lie in wait to surprise a person ap-

[15] Piso, G., and Marcgraf de Liebstad, "Hist. Nat. Brasiliæ," pp. 113–114, 1648.

[16] Bauhin, J., "Hist. Plant. Universalis," 1650.

[17] Du Tertre, J. B., "Historie generale des Antilles," Vol. IV., 1667.

[18] Rochfort, F., "Histoire Naturelle et Morale des Isles Antilles," p. 100, 1681.

proaching along the coast." Rochfort also gives a very poor illustration of a tree with a boar at its root.

Van Rheede, 1678,[19] saw the tree in Malabar where it was called pee-kandel and grows there with five other species of kandel, now all identified as various viviparous trees. The bark was used as a cure for diabetes.

Ray, 1693,[20] gives a long and fairly accurate account of the tree under the head "Mangle Pyri foliis, cum siliquis longis, Ficui Indicae affinis. J. B. (Bauhin) Mangues, seu Mangles; tertia species Guaparaila dicta, Pison. Paretuvier, Rochfort. Oviedus."

"*The Mangrove Tree.*—This tree is among those which are commonly found in Western India, very much selected for the making of buildings and other uses. It grows in marshy places, on the shores of the sea, on the salt flats of rivers. . . . The leaves are similar to the larger leaves of a pear, but thicker and a little larger, opposite to each other, and have a thick mid-rib and many lateral veins, light green. It bears many small flowers on oblong calyces. The pods are two palms long and more, and these are thick, like those of *cassia,* equal to the first and of a rusty color; having a pulp like curds or similar to the marrow of bones, which the Indians, on account of a lack of other foods, feed upon. Even though it is bitter, they prepare it into a healthful food."

Ray then quotes the experience of Oviedo and Clusius in eating it, and goes on to say "the fallen fruit is the food of land crabs rather than men. But the nature of the tree is wonderful, for several grow at the same time and many branches seem to turn down and become roots . . . , which take hold and in turn grow other branches and these, in truth, are no less firmly established than the original trunk of the tree. . . . The wood is heavy and solid and has a brownish bark which is used for tanning leathers instead of oak, as there is no kind of oak found in these lands." The writer goes on and dilates on the uses of the tree and says: "The root of the tree which is soft and moist is split and peeled and applied warm to the poisonous wound of the fish, *Niquus.* It quiets the pain and restores the injured member, but although it may provoke pain

[19] Van Rheede, H., "Hortus Malabaricus," 1678.
[20] Ray, John, "Hist. Plant.," Vol. II., p. 1772, 1693.

in the forehead, it is really a splendid remedy first discovered by the fishermen and given to us by them."

This old chronicler cannot forbear mentioning the honor bestowed on him by Bauhin in naming a fig tree for him and says, "J. Bauhin, who otherwise is not accustomed to be sparing in the subdividing of species, classifies this tree as similar to that famous Indian fig called the Tree of Ray." Among other observations, Ray mentions the yellow tetramerous blossoms as having a honey-like odor and he also is the first to mention the efflorescence of salt on the foliage, for he says: "When the sun shines the leaves of this tree contain a very white salt on their upper surfaces, but when the sky is cloudy, or at night the salt is dissolved and clings like dew, but in the day time being dry and very white it can be collected with the fingers, and from two or three leaves enough can be secured to salt one's broth." As food for animals, Ray says: "Doves and other flying creatures feed on it when there is a lack of better food and from them (the fruits) the flesh of the doves gets so bitter as scarcely to be edible." And in addition to its tanning abilities, the writer says—"it is used daily by the fishermen for dying their nets."

Plukenet, 1669,[21] described *Rhizophora* briefly: "Mangle arbor Pyrifoliis salsis and uliginosis locis in America proveniens; fructu oblongo tereti, summis ramis radicola." He named it the swamp mangrove tree and it is in his writings that it is first called the oyster tree. He quotes Lobez and says also it is called mangu in the Moluccas.

Dampier, 1697,[22] and Gomara[23] both have noted it in their travels and given short descriptions, which are copied by other writers.

Plumier, 1703,[24] mentions it as one of the new genera recently found in America and quotes Piso as the author of the genus. In his description Plumier says the pistil ripens into a turbinate fruit, which sends out a long fusiform seed with its head buried in the fruit. This is the closest observance of the true viviparous nature of the seedling in any of the literature noted thus far. Plumier's

[21] Plukenet, L., "Almagesta Bot.," p. 241, 1769.

[22] Dampier, W., "A New Voyage Around the World," 1697.

[23] Gomara, B. A., cf. Sloan.

[24] Plumier, C., "Nov. Plant. Amer. Gen. Mangles," p. 13, tab. 15, 1703.

figure of the plant is very good and shows the parts dissected. The lenticels on the hypocotyl are also well illustrated.

Labat, 1724,[25] a French missionary, mentions three kinds of paletuviers and says the English and Spanish call them mangles. He says the three kinds are the red, the white and the black; the red and the white being called Raisinier, on account of its raisin-like edible fruit, and the Mahot, respectively. The black paletuvier is evidently the *Rhizophora mangle.* He mentions its laurel-like leaf and states that it grows "5 cens" out in the sea supported on prop roots. "The wood makes good fuel and oysters are borne on the roots which are small but of a good taste."

Sir Hans Sloane, 1725,[26] who was a close observer and a good botanist, describes the mangrove at great length as he saw it in the West Indies. He also mentions almost all the previous voyagers and travelers who have seen this curious tree, as well as his contemporaries, Catesby, Plumier, Dampier and Plukenet. His description is very clear and to the point in that it evidently applies to the "Mangle grande" type. "This Tree rises to thirty or forty Foot high having a Trunc as big as one's Body, and a greenish white, smoothe Bark, with some white Spots here and there. The Tree has very many pendulous Branches swelling towards their Ends, where are placed nine or ten Leaves, set on round them by half Inch long Footstalk, they are four Inches long and two broad, of a dirty green Colour and having one very large eminent Rib running the length of the Leaf; the Flowers stand on an inch long Footstalk, are composed of four thick yellow Petala and as many brown, with some yellow Stamina in the Middle being within covered with a yellow Farina, to which Pod-like Substances, having a Swelling at their Beginning, otherwise exactly like Bobbins with which Bone-Laces are wrought, that Protuberance is rough and a little redish in Colour, about an Inch long, having within a Cavity fitted to receive the small Ends of the Pod-like Substances, and into which they are set, each of them is about six Inches long, beginning slender, swelling by Degrees to near the end where it is Biggest. . . . It has a

[25] Labat, Pere, "Nouveau Voyage aux Isles de l'Amerique," Vol. II., p. 136, 1724.

[26] Sloane, Sir Hans, "A Voyage to the Islands Madeira, Barbados, Jamaica, etc.," 1725.

smooth greenish brown Rind, but a Pith and a fungous mealy Substance and within no Cavity or Seeds and which never ripens or is otherwise than woody."

Sloane then goes on and narrates in detail how the "pod-like substance" germinates and produces other trees. His idea is that a single seed is planted in this "substance" and this grows out until it reaches the mud and becomes a tree. He quotes Piso, Oviedo, Marcgraf, Du Tertre, and says he differs from some of them (Oviedo) in regard to the "Pulp." He has made a thorough search in earlier literature in regard to the "Oyster Tree" and the occurrence of oysters living on the roots and adds his own contribution to the story of the "Oyster Tree." "In the Isle of Trinidad is a Salt River that had Stores of Oysters on the Branches of the Trees, which were very salt and well tasted. All their Oysters grow upon these Boughs and Spraies and not on the Ground." Sloane also adds some new uses to the already manifold application of the mangrove cited before. Among some of the uses he suggests that perhaps the dried buds have been mistaken by mariners for cloves, thus hinting at food and drug adulteration even at that early date. After mentioning the employment of the wood for building purposes and fuel, he says: "The Bark tans Leather well for Shoe Soal, not for Upper Leathers, or Insides, as it is thus tan'd burning the Skin. . . . The Roots serve for dying of Linens and Leaves for Dung. The bark is used by Tanners and Landresses for cloaths, mixed with Oyl like Dirt it is good against Weariness, and with Milk or fresh Butter, outwardly applyd helps them who are diseased in their Livers."

Catesby, 1731,[27] is the last in this series preceding Linnæus to describe the mangrove in the history of his travels. The type Catesby noted is probably only the "chico mangle," as he says they were only 20 to 30 feet tall. His remarks about the general appearance of the tree and flowers is much like Sloane's, but he describes the fruit as being like a "pear at the small end of which hangs a single seed about six inches in length in form like a Bobbin." Catesby, however, is the first to mention the seedlings as floating

[27] Catesby, M., "Nat. Hist. Carolina, Fla. and Bahama Islands," Vol. II., p. 63, 1731.

some distance after dropping from the trees. He also describes the ecology of a mangrove swamp in the Bahamas very well. "In shallow salt Water, these impenetrable Woods of Mangroves are frequented by great Numbers of Alligators, which being too big to enter the closest Recesses of these Thickets, the smaller Ones find a secure Retreat from the Jaws of their voracious Parents. These watery Woods are also plentifully stored with ravenous Fish, Turtles and other Animals which prey continually one upon the other, and the Alligator on them all; so that in no Place have I ever seen such remarkable Scenes of Devastation as amongst these Mangroves in Andros, one of the Bahama Islands, where the Carcasses of half devoured Animals are usually floating in the Water. They grow in most parts of the Earth under the Torrid Zone and are found but little north or south of the Tropicks."

In all the preceding history of the mangrove, the literature naturally falls into two divisions. That from Nearchus (325 B.C.) and Theophrastus (305 B.C.) to Arrian (136 A.D.) embraces the references as found in classical literature, while that from the time Abu 'l Abbas en-Nebaty (1230) to Catesby's (1731) with a few exceptions, who were largely compilers of botanical works, the literature consists of the narratives of travelers, voyagers and explorers. With the stimulus given to systematic studies by the writings of Linnæus and the then recent discovery of new plants in all parts of the world the works of the latter half of the eighteenth century are mostly systematic.

## Taxonomic Relations of *Rhizophora mangle*.

Linnæus[28] in his earlier writings ("Systema Nat.," 1736) had a rather vague conception of the limits of the genera *Rhizophora*. He treated it in the "Systema" and in his "Philosophia Botanica," 1751,[29] under a head "LXII. Candelares" with *Nyssa* and *Mimusops*. These accordingly were later changed and No. 62 was cancelled in the "Philosophia." In the "Species Plantarum," 1753,[30] he gathers all the confused and tangled synonyms and descriptions

[28] Linnaeus, C., "Systema Nat.," p. 442, 1735.
[29] Linnaeus, C., "Philosophia Bot. 62 Candelaria," 1751.
[30] Linnaeus, C., "Species Plant.," Vol. I., p. 634, 1753.

of the early botanists and arranges them in an orderly manner. He recognizes seven species of *Rhizophora,* which he created as a separate genus. These seven species were *R. conjugata, R. gymnorhiza, R. candel, R. mangle, R. cylindrica, R. corniculata* and *R. caseolaris,* all of which are Oriental except *R. mangle.*

For *R. mangle,* Linnæus gives as equivalent the *Mangle foliis acutis* of Jacquin; *Mangle segmentes calycum* of the Wachend ult. 90; *Mangle aquatica* of Plumier; *Mangle pyri foliis* of Sloane and Bauhin; *Mangium candelarium* of Rumph and *Pee-Kandel* of Rheede. In the "Systema" it is No. 592 of the Dodecandria Monogynia and furnished the essential characters of the plant.

Rumph, 1750,[31] a contemporary of Linnæus, gives a lengthy description of his *Mangium candelarium* or *Mangi Mangi* as it occurred in Amboyna of the Moluccas. He also calls it *Mangium candelarium et arcuatum* on account of the resemblance of the hypocotyl to candles and of the prop roots to bows. He also quotes Rochfort's account of this tree or the "Paretewier Tree" and says "Oviedus perceived a great pain in his abdomen from eating the fruits," but mentions a method by which it is prepared for food in the East Indies.

Browne, 1756,[32] in his history of Jamaica mentions the tree as "mangle," and Jacquin, 1763,[33] describes it as *Rhizophora pedunculis bifidis* and faithfully pictures the mangrove thickets of the Antilles region.

Forskahl, 1775,[34] in the Red Sea region says: "Arabes narrarient semen in arbore dehiscere et cotyledones nudos emittere, quod vix credibile mihi videtur," but as he did not actually see this, he did not really describe the plant.

Gærtner, 1788,[35] uses the name of Linnæus, but mentions all the synonyms of preceding authors. Of the embryo he says "inversus, viridus intra semen germinans ejusque integumenta, procresente sua radicula rumpens," showing he realized the significance of vivipary.

[31] Rumph, Geo. E., "Her. Amboin.," Vol. III., p. 108, 1750.

[32] Browne, Patrick, "Civil and Nat. Hist. Jam.," 211, 1756.

[33] Jacquin, N. J., "Select. Stirp. Americ.," 1763.

[34] Forskahl, P., "Flora Ægyptiaca Arabica, Haunice Descrip. Cent.," II., p. 37, 1775.

[35] Gaertner, J., "De Fructibus et Seminibus Plant," 1788.

Jussieu, 1789,[36] used the system of Tournefort, but modified it by adding the new idea of classification which he promulgated by basing it on the positions of stamens and pistils. He placed *Rhizophora* in class XIII. of his fifteen classes. He also recognized but two species—*R. mangle* and *R. gymnorhiza* with *R. caseolaris* as doubtful.

Sarigny, 1796,[37] in Lamarck's Encyclopedia gives a good and accurate account of the family of paletuviers, but recognizes the Linnæus species.

Lamarck, 1804,[38] also recognized the Linnæan species and gives five with *R. mucronata* as a new species. The old *R. corniculata* of Linnæus having now been renamed by Gærtner, *Ægiceras majus* and others discarded so that the Linnæan genus has now been to this extent reorganized. The five species of Lamarck are *R. mangle, mucronata, cylindrica, conjugata* and *candel.*

St. Hilaire, 1805,[39] follows the nomenclature of Linnæus, Jussieu and Lamarck and for *R. mangle* gives the range as both the Indies. It remained for De Candolle to complete the Natural System of Classification and in his Theorie Elementaire de la Botanique, 1813,[40] laid the basis of our modern system. *Rhizophora,* in his "System," is put in Order 57 Myrtineæ. In the "Prodromus," 1828,[41] for the Rhizophoreæ he gives four genera, *Olisbe, Rhizophora, Carallia* and *Cassipourea,* containing in all 14 species. He also treats the old East Indian species of other authors and not synonyms with *R. mangle* of the West Indies.

Velozo, 1827,[42] uses the same nomenclature as Linnæus, but shows an excellent representation of the plant and especially the lenticels on the hypocotyls. The dissection of this organ is also admirably figured.

36 Jussieu, Antoine Lauret, "Gen. Plant.," p. 213, 1789.

37 Sarigny, M., "Lam. Dist.," 4, 696, 1796.

38 Lamarck, J. B. A., "Encyclopedie Methodique, Botanique," Vol. 6, 187, 1804.

39 St. Hilaire, J. H., "Exposition des Fam. Nat. et la Germination des Plants," 1805.

40 De Candolle, A. P., "Theorie Elementaire de la Botanique," 1813.

41 De Candolle, A. P., "Prodromus Syst. Naturalis," Vol. III., 31–34, 1824.

42 Velozo, di Miranda J., "Floræ Fluminensis Icones," 1827.

Bartling, 1830,[43] devised a system of classification in which the Rhizophoreæ were removed from the Order Myrtineæ and put under one called Calycifloræ, *i. e.*, on account of its structure it was placed with the Vochysieæ between the Onagraceæ and the Combretaceæ.

Endlicher, 1836,[44] used a modified system of Jussieu's, but the changes were largely in the great subdivisions, the genera are still those of Bartling more particularly.

Brongniart, 1843,[45] transposes and enlarges the family of Rhizophoreæ and places it in an order *Œnotherinæ* with Lythraceæ and Myrtaceæ as a doubtful member.

Meisner, 1843,[46] groups the Melastomaceæ, Lythraceæ, Onagraceæ, Combretaceæ and Vochysieæ with the Rhizophoraceæ as class 16, Calcycanthemoe.

Lindley, 1845,[47] reorganized the group and under the head Myrtales united ten families, one of which was the Rhizophoreæ, thus recogninzing its affinities with the Myrtales, on account of its "plurilocular ovary, polypetalous flowers, valvate calyx, indefinite stamens and flat cotyledons much shorter than the radicle, which germinates before the fruits fall." He recognizes five genera.

Grisebach, 1864,[48] mentions only *R. mangle* as being found in the western hemisphere and says that Meyers's *R. racemosa* is synonymous.

Hemsley, W. B.,[49] in his reprint on the "Voyage of the *Challenger*" regards the *R. mangle* as the only *Rhizophora* in the Americas.

Hooker, 1879,[50] in the Flora of British India does not include *R. mangle,* but it is known to occur in the Pacific Islands and follows there certain lines of dissemination.

[43] Bartling, Fr., "Ordines Nat. Plant.," 1830.

[44] Endlicher, S., "Gen. Plant. Sec. Ordines Nat. Pis.," 1836.

[45] Brongniart, Adolphe, "Enumeration des Genres des Plantes cultives," 1843.

[46] Meisner, C. F., "Plant Vascularium Gen. Secund Ordines, 1843.

[47] Lindley, John, "Vegetable Kingdom," p. 726, 1845.

[48] Grisebach, A. H. K., "Flora of British West Indies," p. 274, 1864.

[49] Hemsley, W. B., "Voyage of H. M. S. *Challenger,* Bot. Bermudas," p. 32.

[50] Hooker, D. J., "Flora of British India," Vol. II., p. 435, 1878.

Engler and Prantl, 1898,[51] regard the group Rhizophoreæ as having only five genera with *Rhizophora* composed of three species —*R. mangle, R. conjugata* and *R. mucronata.* This classification is that used in all Floras containing the species.

Small[52] in all his manuals[53, 54] mentions only *Rhizophora mangle,* as well as Chapman[55] and other systematic writers.

The family Rhizophoraceæ then belonging in the Myrtales order, falls naturally into two subfamilies—Rhizophorideæ and the Anisophylloideæ. This is recognized by De Candolle,[56] and Van Tieghem[57] and all the later writers on the family. Some authors, however, divide the family into a triple grouping, with a third head the Legnotideæ, and still others as Baillon[58] arrange the family in a different grouping. This latter author divides fourteen genera into four divisions—I. Rhizophoreæ, II. the Baraldieæ, III. Macarisieæ, which is equivalent to the group Legonatideæ of Bartling and Cassipoureæ of Meisner, and IV. the Anisophylleæ. The affinities of the plants in this family have manifold connections such as the Onagraceæ, Loranthaceæ, Cornaceæ, Lythraceæ, as may be seen by the placing of these genera by the earlier authors cited above, and before R, Brown's, 1814,[59] arrangement had been placed in the Caprifoliaceæ. All the groupings have been based largely on the relative positions of the perianth and the gynœcium, Baillon's group of Rhizophoreæ having concave receptacles and ovary inferior. Style simple and seed exalbuminous, with macropod embryo, germinating in fruits on the trees, embraces four genera. These are the ones mostly given in modern floras of oriental countries and are *Rhizophora, Ceriops, Bruguiera* and *Kandelia.* They are all representatives of tropical Asia and Africa, except *Rhizophora,* which is cosmopolitan in the tropics.

[51] Engler, A., and Prantl, K., "Die naturlichen Pflanzenfamilien," Teil III., abt. 7, p. 42, 1892.

[52] Small, J. K., "Flora of S. E. United States," p. 834, 1908.

[53] Small, J. K., "Shrubs of Florida," p. 89, 1913.

[54] Small, J. K., "Flora of the Florida Keys," p. 105, 1913.

[55] Chapman, J., "Flora of Southeastern United States," p. 152, 1897.

[56] De Candolle, C., "Prodromus," III., p. 31.

[57] Van Tieghem, Ph., *Ann. Soc. Nat.,* Ser. 7, T. VII., p. 376, 1888.

[58] Baillon, H., "Nat. Hist. of Plants," Vol. VI., p. 287.

[59] Brown, R., "Flind, Voy.," II., p. 549, 1814.

Engler and Prantl, however, whose classification is still the authority perhaps includes under the division of the family Rhizophorideæ-Gynotrochinæ, five genera, *Crossostyles, Gynotroches, Rhizophora, Ceriops* and *Kandelia.*

But though the genera of the Rhizophoraceæ do not fall very naturally into an arrangement, it is now fairly well decided that the seven species of the Linnæan genus, *Rhizophora,* have been condensed so that only three species are recognized, viz., *R. mangle, R. conjugata* and *R. mucronata.* Of these three species as noted before only *R. mangle* is indigenous in the Americas, although Martius, Euler and Urban,[60] 1882, in the "Flora Brasiliensis" mentions Meyers's species *R. racemosa.* This is a synonym or a subspecies of *R. mangle.* Guppy, 1906, "recognizes *R. mangle* under two distinct types—the "Grande" and the "Chico" types. This will be discussed in a subsequent paragraph.

The main features which demarcate *R. mangle* from its related species are the shapes of the leaves, the length of the petioles and the number of flowers in the cymes; and the texture of the petals, whether they be thick lanate, or thin and glabrous. There has been some slight confusion in the nomenclature of these three species, although recent floras have straightened out the tangle. Timmens, 1894,[62] in his "Flora of Ceylon," mentions the two Oriental species, and gives as one—*R. mucronata* Lam. as synonymous with *R. candel* Moon Cat and *R. macrorhiza* of Griffiths. The other of his two species is *R. candelaria,* which is synonymous with *R. conjugata* of Linnæus and *R. mangle* Moon Cat and Linnæus in part.

Hooker,[63] in "Flora of British India," also gives *R. mucronata* as the *R. mangle* of Linn., but this is not correct. The *R. mangle,* which is the equivalent of *R. mucronata* Lam., is *L. mangle* Roxb., which is quite different from *R. mangle* of Linnæus. This error of nomenclature has been made by Roxburgh and perpetuated in the older works.

[60] Martius, Euler and Urban, "Flora Brasiliensis," Vol. XII., par. II., p. 425, 1882.

[61] Guppy, H. B., "Observations of a Naturalist in the Pacific," Vol. II., 1906.

[62] Timmens, H., "Flora of Ceylon," Part II., p. 151, 1894.

[63] Hooker, D. J., "Flora of British India," Vol. II., 435, 1879.

King[64] has this point clear in his Malayan Flora, where he says *R. mucronata*—*R. mangle* Roxb. (not Linn.) and also *R. macrorhiza* Griff. while *R. conjugata* Lam.—*R. candelaria* of De Candolle.

*R. mangle* Linn. is a purely American species, but has been found by Guppy associated with the Oriental species in some of the islands in the South Pacific.

## Morphology and Histology.

The gross morphology of *Rhizophora mangle* is synopsized in any flora or manual of the species of the tropics in which the plants are found. But it is well perhaps to set down the chief features of their structure here. (See Plate IX.) The red mangrove may be a large tree 60 to 80 feet tall, or smaller shrub 6 to 18 feet tall. This varies with the region and has given rise to the two types based on size, *i. e.*, the "*Mangle chico*" and "*Mangle grande*." The primary root soon dies out, secondary roots are put out by the seedling. Later adventitious prop-roots are put out from the base of the stem and from a mass of arched stilts about the tree. The branching is opposite and from the lower branches aërating roots are let down to the substratum, these also assist the prop-roots in anchoring the tree. The twigs are stiff, cicatrized and thick, and the wood throughout the tree is very hard and dense.

The leaves are opposite, clustered on the ends of the twigs and furnished with large inter-petiolate and caducous stipules. They are decussate, petiolate, elliptic, entire, glabrous thick and coriaceous.

The flowers are yellowish or whitish, coriaceous and axillary; collected into bi- triparous, rarely simple and more generally ramified cymes at the summit of a common peduncle. These flowers are usually pedicellate, articulate and have mostly two connate bracteoles forming a sort of involucre. The flower is regular with a concave obconical receptacle. The sepals are four in number inserted on the margin of the receptacle, coriaceous and valvate; and the petals are also four, alternate with the sepals and valvate. The stamens are mostly eight, with four larger ones oppositipetalous, and have many short filaments or none at all. The anthers are unique. The anther

[64] King, Geo., "Materials for a Flora of the Malayan Peninsula," Vol. 3, p. 313, Calcutta, 1902.

furrows are lateral or subintrorse and the pollen sacs are areolate-multilocellate.

The ovary is half inferior, bi-locular and at the vertex produced into a cone. Style subulate, sometimes rather short, at the apex stigmatose and bidentate. There are two ovules in each cell, placed in a collarterally descending position, the micropyle being extrorsely superior.

The fruit is berry-like, coriaceous and indehiscent, surrounded below the middle by the reflexed persistent calyx. Only one ovule matures into a seed. The embryo is exalbuminous with fused cotyledons. The radicle or hypocotyl perforates the apex of the seed and germinates within the fruit; at length pushing out through the pericarp, greatly elongates while still on the tree. An absciss layer is finally formed at the junction of the cotyledonary sheath and the shoulder of the hypocotyl, and the seedling drops from the parent tree into the mud or water.

## The Roots.

The roots of the *mangrove,* even as mentioned by the ancient Greeks, are a peculiar feature of the genus, being, as Theophrastus says, like "polypi." The primary root put out by the radicular end of the hypocotyl soon stops growth and the root function is given over entirely to secondary roots. The cause of cessation of growth by the primary roots has been suggested by Warming,[65] Johow,[66] Schimper,[67] and others, as due to the bites of crabs, snails or other mechanical injury. At any rate the primary root does not long persist and the plant is soon anchored by a rich mass of secondary roots. The structure of the roots is very interesting. There are really two types of roots, those prop-roots arising from the base of the tree and bending out to form the curved stilts, and the adventitious roots dropped from the lower branches are one kind and are known as the aërial or aërating or pneumatophore roots, while those

[65] Warming, Eug., "Rhizophora Mangle, Tropische Fragmente," *Engler's Jahrb. für Syst.,* Bd. 4, p. 520.

[66] Johow, Fr., "Vegetationsbilder aus West Indien und Venezuela, Die Mangrove Sümpfe, Kosmos," Bd. I., pp. 415–426, 1884.

[67] Schimper, A. F. W., "Indo-Malayische Strandflora," *Bot. Mitheilungen aus des Tropen,* Heft 3, 1891.

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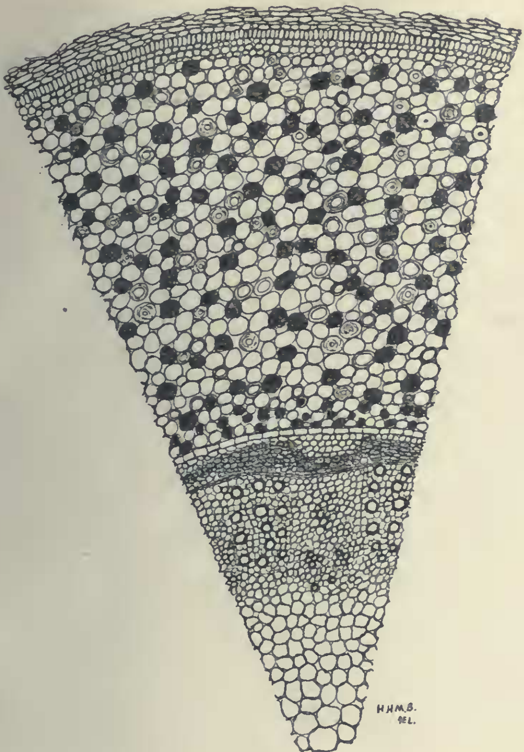

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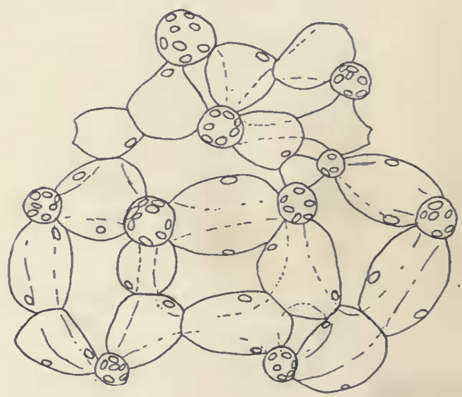

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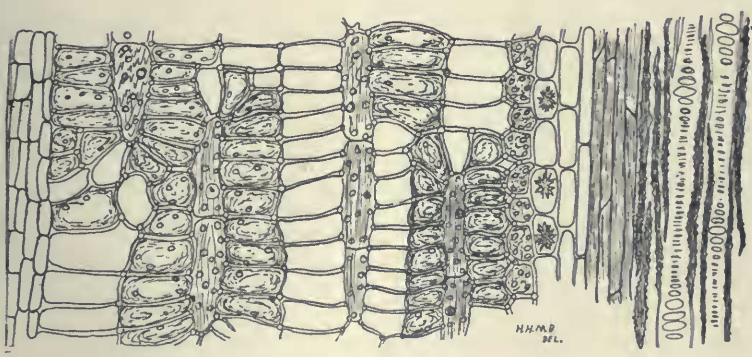

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FIG. I. Transverse section of prop-root, showing cortex containing idioblasts, tannin cells and parenchymatic cells. Cork ouside and the endodermis on the inner margin of the cortex. The vascular cylinder and medulla inside. × 106.

FIG. 2. Camera lucida drawing of longitudinal section. Cortex cells showing sections of idioblasts and tannin cells. × 470.

FIG. 3. Enlarged transverse section of cortex cells of absorptive root. Large elliptic cells transfusion tissue smaller circular cells, longitudinal cells containing starch. × 600.

FIG. 4. Drawing (cam. luc.) of longitudinal section absorptive root. × 96.

which are subterranean or submarine, buried in the mud, and which have assumed a purely absorptive rôle, are called the absorptive roots in this paper. Van Tieghem[68] has described and figured the root of the *Rhizophora,* and shows especially the development of these secondary roots. He says: "An arch of the pericycle of the width of three cells in the external layer and corresponding with a wood bundle, increases and cuts off two rows of cells, but especially does the external layer increase, and it is this alone, by two tangential wall formations, which differentiates the three regions of the rootlet from the original cells. The internal row does not go beyond the base of the central cylinder. The superimposed arc of the endodermis dilates its elements, but not radically, and encloses the developing rootlet by an absorptive pouch. In this pouch, which is dilated to a great extent, the rootlet elongates rapidly the width of the cortex, but remains very narrow. More slowly it then enlarges at the summit and the pouch is absorbed laterally, but the terminal part is left adhering like a cap as it emerges from the root."

This interesting process may be seen on both the hypocotyls of seedlings and the origin of the dependent prop-roots from the branches. These little root caps adhere for quite a long period, especially in the aërating roots. If the tip of one of these pendant roots is injured, there will be a division just back of the tip and the geotropic growth will continue as two or three branches. These branches usually push out at the lenticel with which these aërating roots are well supplied. The same thing occurs on the hypocotyl which also is supplied with lenticels. If the roots at the radicular end are destroyed adventitious roots are put out up farther on the hypocotyl, perhaps just a few centimeters below the plumule. What the stimulus may be is not exactly known in this case, but in as much as oxygen has been shown to be stimulating in the production of root hairs in plants, it may be presumed that the supply of oxygen received through the lenticel acts as a stimulus for the production of the rootlet from the pericambial tissue just at the point beneath the lenticel. The initial stimulus for the production of these adven-

[68] Van Tieghem, Ph., and Douliot, H., *Ann. des Sci. Nat. Botanique,* Ser. 7, Tome 7, p. 212.

titious roots is, of course, the injury or removal of the tip of the root.

Root hairs are lacking in *Rhizophora,* as in most all aquatic plants, but their function is fulfilled by many tiny roots which grow out from the subterranean or submarine absorptive roots. These absorptive roots are quite different from the aërial part of the prop-roots or those dependent from the branches (see Fig. 4 and 6, Pl. VIII.) These roots are mostly rather short and thick, fleshy, and whitish or pinkish in color, and of a soft texture.

The extra thickness of these subterranean absorptive roots is due to the greater development of the primary cortex. In the absorptive root this is of large loose cells with very large open intercellular spaces in which idioblasts or trichoblasts are lacking. Externally as Solereder[69] has shown, the periderm consists in this absorptive root only of cork cells, while the same tissue in the aërial portion has both cork and "parenchymatic separation tissue" alternating.

The cortex of large round cells has been studied by both Van Tieghem and Solereder, and even figured; but it is supposed that the material was not fresh and the delicate cells of the cortex were shrunken (Pl. IV., Fig. 3). These cells are closely connected with the absorption of water, presumably growing as the plants do in salt water of a rather high concentration, shrunk on being placed in reagents of different densities. At least in the preparation of material for this paper such has been the case and only in material freshly sectioned and mounted in glycerine water could the true idea of the structure of this cortex be gained. The cells compose a loose network and have very large open spaces between them. Some cells are converted contiguously in strands, others radiate about short groups of cells, which are much elongated in the direction of the axis of the root (Pl. I., Fig. 4). These elongated cells are often quite full of starch grains, while the large roundish turgid cells radiating from them contain relatively few starch grains and more mucilaginous protoplasm which stains slightly with water eosin. These round cells, when slightly shrunken due

[69] Solereder, H., "Systematische Anatomie der Dicotyledonen," p. 384, 1889.

to a partial plasmolysis, show, on focusing at different levels, the lower wall and its line of juncture with a cell beneath or on the side, this artifact produces a double line of tension or wrinkle on the wall which seems like a tube or channel contained within the cell. Warming regarded these as thickenings for support within the cells which prop the cells apart and assist the soft tissue of the root in maintaining its shape and as they do not appear along the wall separating an intercellular space this artefact seems to really confirm this view. But since these "verdickungsleisten" are not seen in freshly sectioned and water mounted material, Warming's theory of lateral mechanical support for these cells is not tenable. Material carried up in balsam or glycerine jelly does show this peculiar irregularly "branched thickening," but it can only be regarded as an artefact. The tissue of this cortex seems to function as a transfusion tissue. Warming and Solereder also both state that the trichoblasts are lacking in the absorptive and tertiary roots, but on close examination some may be found scattered in the xylem elements of the vascular bundle.

In the aërating prop-roots and those dependent from the branches which have not yet reached the water the cortical area is filled with trichoblasts and large tannin-containing cells (see Figs. 1 and 2, Pl. IV.). These trichoblasts are frequently branched and double or H-shaped, the branches running up in the intercellular spaces. The tannin cells are larger than the cortical parenchyma cells and on longitudinal section appear as long chains of dense, dark, solidly filled cells.

The endodermis is easily recognized in either transverse or longitudinal sections by its loose clear structure, the walls being thin and rather more regular than the cells of the cortex, and show the slight irregularities in the wall that Warming mentions and calls "the Caspar spots." In the older roots the endodermis is crushed by the secondary growth so as not to be recognizable.

The central vascular cylinder of these aërating roots shows several interesting peculiarities. If sections are made from regions just behind the root cap and then a region several centimeters back and finally of an older root, striking differences are noted. In the figure given (Fig. 1, Pl. IV.), the section has been cut about three centimeters behind the cap. The conductive bundle cylinder is composed of about 30 or 40 alternating strands of xylem and phloëm tissue. As Warming has also shown, however, a most unusual departure is made from this regular root arrangement in that there are often more than one phloëm strand between two xylem patches, as seen in transverse section. This is supposed to occur by the splitting of strands. The phloëm strands contain both sieve tubes and phloëm parenchyma. The xylem in its earliest state, *i. e.*, protoxylem, has very few spiral tracheæ, just behind this externally is a small group of soft bast elements, the tracheæ being surrounded by a sclerenchyma ring or sheath. In this development, the method of growth is centrifugal. Beyond this group of phloëm elements is the xylem strand and this has the peculiar structure of a double bundle, but both are enclosed in one sclerenchyma sheath. What causes this splitting in the xylem it is not possible to say. Among the xylem elements are scattered large pitted and scalariform vessels. The phloëm is now very well developed.

The pith of the root is of large thin-walled cells, typical medullary tissue with intercellular spaces in which lie many trichoblasts. The pith also contains tannin cells.

## The Stem.

The twigs and branches of *Rhizophora* show little that is peculiar in the general arrangement of the structures. In the wood, however, there are prosenchymatic vessels which are pitted and also there are some vessels which have ladder-like perforations. These appear as holes with transverse bars across which in most instances number about four or five. The medullary rays are rather broad and where the bundle vessels come in contact with the ray tissue the walls of the former are pitted.

The cork formation, according to Solereder and Möller,[70] is superficial, and of the spongy type. In the pericycle there is a dense ring of sclerenchyma, which makes the twigs very difficult to cut.

[70] Möller, J., "Holzanatomie," *Deutschr. Wiener Akad.*, p. 103, 1876.

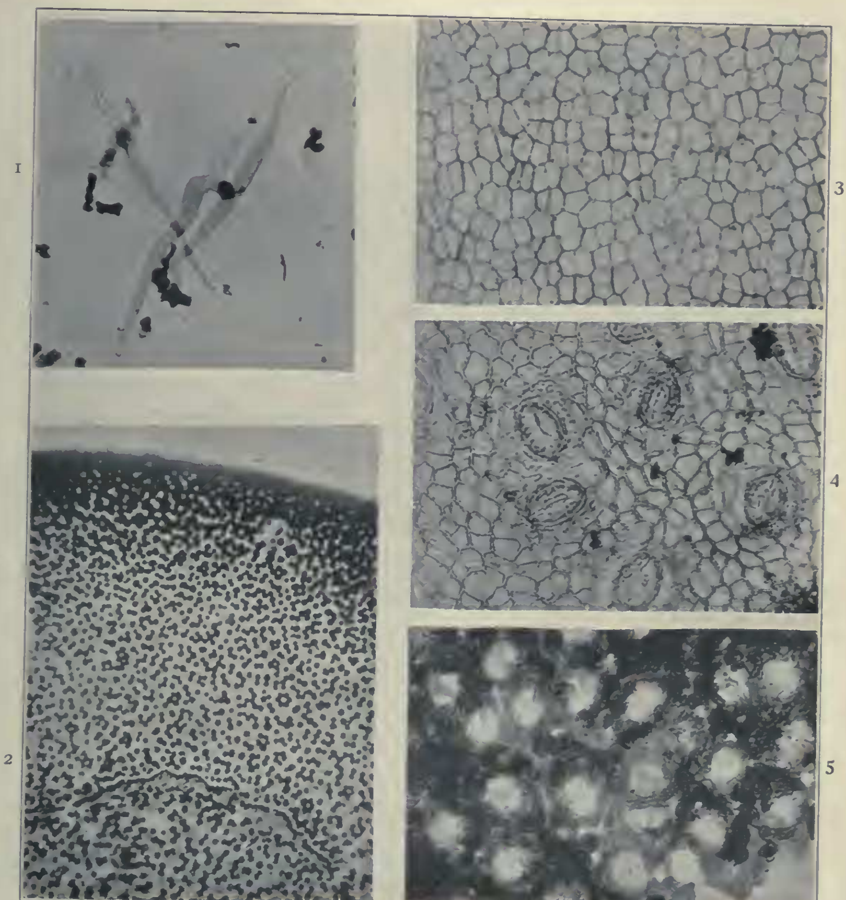



FIG. 1. Idioblasts from macerated leaves. Micro-photograph, × 175.

FIG. 2. Transverse section hypocotyle stained with copper acetate. Tannin cells black. × 18.

FIG. 3. Micro-photograph of upper epidermis. × 175.

FIG. 4. Lower epidermis, showing stomata. Micro-photograph, × 175.

FIG. 5. Lower epidermis with cells of the hypodermis shown. Dark cells stained for tannin, light areas stomata. Micro-photograph, × 175.

## The Leaf.

It is in the leaf that a great many of the adaptations of the *mangrove* to its special environment are seen. The leaves, as mentioned before, are opposite and assume somewhat a perpendicular position. Johow[71] regards this position as a protection against the light, the great intensity of which has, according to him, a destructive effect on the chlorophyll. Each pair of leaves is provided with two interpetiolar stipules which are twisted in the opposite direction from that of the leaf which it encloses. The unfolding of the leaf blade from the stipule occurs as in the figs. The stipules are provided with glandular hairs, which secrete a resin-like substance that Eggers[72] says covers the plumule in the seedling stage and protects it against the action of the water when the seedling floats in the sea.

Warming[73] figures a diagram of the cross section of a petiole in which there is a ring of vascular tissue and inside this ring are several other vascular bundles with the phloëm turned in the reverse direction. In his opinion these strands arose as splits from the bundles on the upper side.

The leaf blade is elliptic and has a very prominent midrib, as Sloan[74] observed in his early description. The epidermis is very heavily cutinized, especially on the upper side which entirely lacks stomata (Fig. 3, Pl. V.). The stomata are slightly sunken and provided with an antechamber (Fig. 4, Pl. V.). According to Warming the stomata originate at different times, the younger between the older ones, and are scattered in every direction. A most striking feature of the leaf tissue is the large, mostly four-celled water-storage hypodermis. This is a true hypodermis, as may be seen in examining young leaves still rolled in the stipules, which even here show a number of layers of these cells. The upper layer of the hypodermis or mostly the two uppermost layers are filled with tannin (Fig. 5, Pl. V.). The function of these tannin

[71] Johow, Fr., loc. cit., p. 419.

[72] Eggers, H., "*Rhizophora mangle* L., Videnskabelige, Meddelelser," p. 180, 1887.

[73] Warming, Eug., "*Rhizophora mangle* L., Tropische Fragments," II., *Engler's Botanische Jahrbucher für Systematik*, Bd. 4, 1883, p. 319.

[74] Sloan, H., "A Voyage to the Island Madeira, Barbados, Jamaica, etc.," 1725.

layers as a light screen will be considered in the physiology. On account of the development of the hypodermis, the palisade lies deep in the mesophyll, in fact almost in the middle of the leaf. There are usually three layers of very narrow elongated palisade cells. Interspersed among them are many branched and often much twisted trichoblasts. These branches ramify about in intercellular spaces and push the cells aside as they grow. The spongy tissue of the leaf is rather loose and is composed of cells varying a great deal in size. Some are large and contain tannin and others contain only a thick mucilaginous protoplasm. Large spherical, many pointed crystals of calcium oxalate fill up cells scattered in the spongy tissue, as well as the water hypodermis (see Fig. 4, Pl. VII). Warming thinks the shining, thick epidermis of the leaves helps to reflect the intense light and doubtless this is true and, as will be shown in the physiology, this reflection serves an important service.

On the under surface of the leaves are many small black specks, which Warming regarded as the opening of glands located deep within the spongy tissue. These were filled with a secretion which looked brown in the material he examined, *i. e.*, material pickled in alcohol. It has now been shown that these tiny specks are not glands, or glandular hairs, or disks, but really small bodies of cork which are formed from the epidermal cells.

## The Flower.

The inflorescence has already been described as usually di- or trichæsial cymes, and its relation to the axis and the bracts has been well described by other authors. The four stiff woody sepals which persist and grow in size as the fruit develops are heavily impregnated with stone-cells or trichoblasts. In the lower part of the receptacle below the junction of the sepals and the ovary, *i. e.*, just beneath the ovules, there is a large mass of very loose tissue, which Griffith[75] noted in his early papers on the species. This tissue has very large intercellular spaces to permit the rapid growth of the embryo to take place without unduly crushing the cells of the fruit. The four petals placed alternately with the sepals are early deciduous. They, as well as the sepals, are valvate and on their

[75] Griffith, W., *Trans. of the Med. and Phys. Soc. of Calcutta.*

inner faces are thickly supplied with unicellular hairs. These hairs have been shown in the illustrations of Baillon,[76] but in most of his other diagrams there are great errors, as Warming, who has done most excellent work on the species, is careful to point out. In the bud the petals are slightly curved down over the tips of the anthers. The tissue of the petals does not contain trichoblasts, but the cells do contain protoplasmic constituents, which take stains more readily than the cells of the other parts of the flower.

The eight anthers are almost sessile and at the base of the very short filaments there is a ring of nectary glands (see Fig. 1, Pl. VI.), which secretes abundant nectar that is eagerly collected by insects. In sections these nectar glands are seen as dense deeply stained masses which have delicate vascular connections with the strand which passes up into the anther and also into the petals. The anthers, as mentioned before, are multilocular, and this feature has been described by many previous botanists. Griffith[77] early gave a good description of the method of dehiscence by the pulling away of the valves and exposing the core filled with loculi, "resembling *Viscum* in this circumstance." Goebel[78] describes such chambers in the anthers of *Gaura* and *Clarkia* in the Onagraceæ and regards them as the homologues of the trabeculæ of the sporangia in *Isoetes*, their function being to nourish the sporogenous tissue. Wight[79] also gives a very clear description of this form of pollen arrangement and dehiscence and figures it in another place.[80]

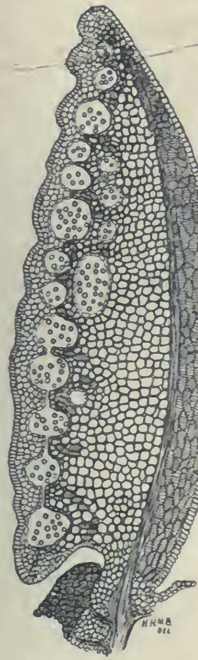
The anther on close examination has two introrse faces and the two slight grooves down the length of these faces, where the thin exothecial membrane ruptures and then rolls back in ordinary anthers. The pollen alveoli are small round cavities embedded in the connective tissue, which is much enlarged in these anthers. The two delicate channels on the faces of the anthers finally disappear with the growth of the tissue in many cases and dehiscence may be by a suture at the medial line or at their lateral lines.

Warming has pointed out the two special features in the forma-

[76] Baillon, H., "Natural History of Plants," Vol. VI., Fig. 256.
[77] Griffith, W., loc. cit., Pl. 640, Fig. 11.
[78] Goebel, K., "Organographie der Pflanzen," p. 731, 1898.
[79] Wight, Robt., "Illustrations of Indian Botany," Vol. 1, 207, 1840.
[80] Wight, Robt., "Icones Plant. Indiæ Orient," 1, tab. 238–240.

tion of the chambers and later of the pollen from the very young parenchymatic tissue. These are first that the two pollen sacs fuse in the upper part of the anther where there is no bilateral arrangement by a median line, but a line of chambers occurs in the middle plane of the apex; the second is that not all the cells of the young anther parenchyma or endothecium become sporogenous as they do in other anthers, but some cells become the alveolar walls. Warming further remarks that in his opinion this is not an old phylogenetic condition but a recent adaptation and is seen in not only the mangroves, *Rhizophora, Ægiceras,* etc., but in other families as the Onagraceæ above mentioned and the Orchidaceæ (*Phaius* and *Bleteia,* etc.), as well as *Viscum* of the Loranthaceæ.

The mechanism of the dehiscence, however, is just as interesting as the formation of these peculiar anthers and their pollen. This feature was brought out in examination of the cellular structure of the bud. As the other workers on the species have shown, the anthers in transverse section are triangular, or obovate-triangular with the dehiscing faces introrse and the back or outer side of the anther is a broad expansion of the connective (Fig. 2, Pl. VI.). This connective area, as well as the partitions of the pollen loculi contain a peculiar kind of cell. All the previous investigations have overlooked these cells. They happened to be brought out in sections which had been double-stained in safranin and methyl-green to contrast the lignified walls of the idioblasts. While examining these sections there was noticed in the outer cells of the connective area of the anther a layer of cells which contained peculiar lignified, transverse ring thickenings inside the cellulose wall (see Figs. 3 and 4, Pl. VI.). In these anthers this reinforced area extends clear to the tip and the cells composing it are rather elongated. According to our interpretation, these cells play an important mechanical part in the dehiscence of the pollen. As the pollen ripens in the loculi, the thin exothecium shrinks and while this is taking place the strain produced on this thin-walled cell layer, particularly along the middle line of the pollen loculi, by the rigidity of the areas composed of the reinforced cells, a rupture occurs at the weakest places, *i. e.,* at the middle line where the partitions are thinnest. When the split has occurred all along the line the exothecium falls



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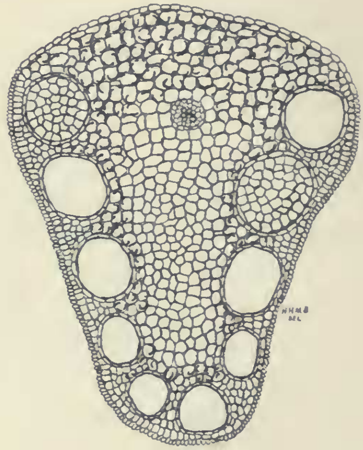
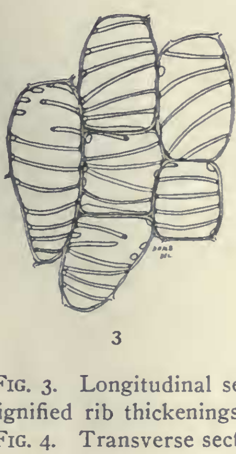


2

FIG. 1. Longitudinal section of anther showing area of reinforced cells on outer side, vascular tracts, pollen loculi with reinforced cells in the septa, and thin exothecium separating off. Pollen grains in loculi and dark cells of nectary at base of stamen. (Cam. luc.) × 70.

FIG. 2. Transverse section of anther showing pollen loculi, vascular bundle, and areas of reinforced cells. (Cam. luc.) × 340.



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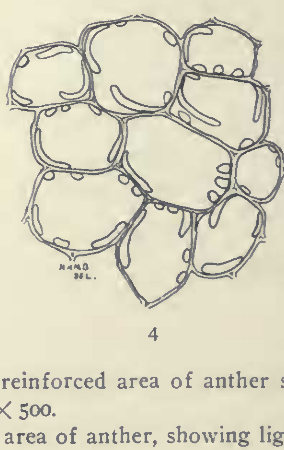

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FIG. 3. Longitudinal section of cells of reinforced area of anther showing lignified rib thickenings. (Cam. luc.) × 500.

FIG. 4. Transverse section of reinforced area of anther, showing lignified ribs. (Cam. luc.) × 500.

away, just as described by previous writers, and exposes the pollen in the loculi to the air and contact of insects. The cells here described with their lignified thickenings are also densely filled with dark-staining protoplasm, similar to those of the petals. According to Warming the cytological development of the pollen grains does not present any unusual feature and the cursory examination of it in the preparation of this paper, which is not concerned with cytological details, seems to confirm Warming's statement.

The pistil is relatively simple and has a two-celled ovary with the spongy tissue above mentioned beneath it. In each of these two cells there are seen two ovules, one of which becomes a seed. The ovary tapers gradually into the erect and elongated woody style which has a bifid stigma at the tip. The ovary, the ovules, the egg and fertilization apparatus have a very special interest in *Rhizophora* owing to the plant's habit of vivipary. The endosperm itself has been the subject of investigation and considerable speculation. Baillon seems to have started the discussion by saying that the embryo is destitute of albumen, but is surrounded by a soft matter which assumed its rôle. These parts connected with the reproductive function are best considered under the next heading.

## Embryology.

The embryology of the red mangrove has been attacked by several botanists with more or less success. The study of its vivipary has led up to these detailed studies, which have been made principally by three workers, Warming,[81] 1883, Karsten,[82] 1891, and the most recent by M. T. Cook,[83] 1907. The first merely touched incidentally on the embryology in as far as it was related to the general morphology. Karsten's work, while more detailed, was undertaken with a view to its relation to vivipary and the ecology of *mangroves* in the widest sense. Cook's paper summarizes the work of Karsten and while short is very good, but the author himself says that com-

[81] Warming, Eug., loc. cit., p. 528.

[82] Karsten, G., "Ueber die Mangrove-Vegetation in Malayahn Archipel.," *Bibliotheca Botanica,* Heft 22, 1891.

[83] Cook, M. T., "The Embryology of *Rhizophora mangle,*" *Bull. Torr. Bot. Club,* Vol. 34, No. 6, p. 271, 1917.

plete series were lacking in his studies owing to deficiency in material. In this resumé, the rather specialized paper by Haberlandt[84] and to some extent the studies of Johow[85] cannot be overlooked. The former was particularly concerned with the nourishment of the embryo and the function of the endosperm.

In this paper the embryology has not been considered as being of primary consideration in relation to the studies of the physiology of the species and in view of the investigations already made on the embryology the main features will only be reviewed here to give a clearer understanding of the morphology. A few photomicrographs are given also by way of illustration.

The ovules all show a nucellus and in the tip of this, which in cross section is slightly irregular in outline, there is the archesporium. Cook says this is subepidermal and figures it as such. This archesporial cell cuts off two tapetal cells, but this number does not appear to be definitely known for the genus. However, Karsten's material *R. mucronata* is figured as having two tapetal cells and Cook's material *R. mangle* also. In the figure of the longitudinal section given in this paper the large horseshoe shape section of the integument is seen as the only one present. Cook has shown that there really are two integuments at the beginning where the archeporial cell is still small, but that later the inner one is destroyed. The integuments both grow rapidly and soon enclose the nucellus, while the archesporium divides into the megaspore cells. Here there seems to be a discrepancy in the number for the genus, as Karsten found four for *R. mucronata,* while Cook gets three for *R. mangle,* but as Cook says he only was able to secure one good preparation of this stage the constant number cannot positively be stated. As the embryo sac enlarges the nucellus completely disappears, as does also the inner integument with growth of the sac.

This stage, or one a little later, is shown in the figure where the outer integument is seen with a littte of the soft spongy endosperm inside and the enlarged embryo, with the tiny dark area where the plumule is beginning to form. The cells of the endosperm

[84] Haberlandt, G., "Ueber die Ernährung der Keimleinge, etc.," *Ann. du Jardin Botanique de Buitenzorg, Treub,* Vol. 12, p. 91, 1895.

[85] Johow, Fr., loc. cit.

seem to radiate from a more or less definite center of growth in the sac, as Cook has mentioned. This feature is seen in the figure of a transverse section of the ovules.

The function of this endosperm has engaged the attention of the various botanists mentioned above. The cells themselves are large and loose and are easily distinguished from those of the enclosing integument and Warming[86] says they appear as if empty of contents and that he never found starch in them, but had noticed sphærocrystals and it is furthermore remarked by this author that its function does not seem to be that of food storage, but its later development indicates a quite unusual function. This later development is the pushing out of the endosperm and the cotyledonary end of the embryo through the micropylar end of the sac or what now remains of it as the outer integument, into the ovarian cavity to form an arillar collar or outgrowth. As Warming and Johow[87] both agree, the function of this structure is not for the luring of animals for the purpose of seed dissemination, as other arils in *Myristica, Casearia* and *Euonymus,* but, as Warming says (p. 531), "Bei *Rhizophora* wird das extraovulare albumen wahrscheinlich dazu dienen, als Saugorgan dem Keimlinge Nahrung von der Mutterpflanze zuzuführen." This peculiar endosperm structure is seen not only in the Rhizophoraceæ but in other viviparous plants, as Treub[88] has shown for *Avicennia,* etc. Karsten[89] has shown the same conditions for *R. mucronata, Bruguiera, Ceriops, Ægiceras,* etc., and that these plants all follow the same development as was early recorded by Hofmeister[90] in the origin of the embryo sac from the nucellus, etc. Karsten divides the endosperm formation into two categories; first that form in which the embryo is soon anchored near the micropyle and only after this does the endosperm, in very small amounts, begin to form from unconnected cells of a foamy consistency. In the second category to which *Rhizophora* belongs

[86] Warming, Eug., loc. cit., p. 531.

[87] Johow, Fr., loc. cit., p. 421.

[88] Treub, M., *Annales du Jard. Botanique de Buitenzorg,* Vol. 3, p. 79, 1882.

[89] Karsten, G., loc. cit., p. 31.

[90] Hofmeister, W., "Neuere Beobachtungen über Embryobildung bei Phanerogamen," *Pringsheim's Jahrb.,* I., p. 82, 1859.

the endosperm completely surrounds the unanchored embryo and permits of motion in different places by the growth of the embryo. Of both these cases Karsten says (p. 33, l. c.): "Die Rolle eines Reservestoffe speichernden Gewebes kommt aber dem Endosperm weder im ersten, noch im zweiten Falle zu."

It remained for Haberlandt, however, to do the most intensive work on these endosperm cells. The plants which he investigated at Buitenzorg were *Bruguiera, Ægiceras* and *R. mucronata*. For the first two genera he has learned that the endosperm forms many-celled haustoria, which grow into the tissue of the integument and absorb the food for the embryo (p. 95, l. c.). However when he came to *R. mucronata* he expected to see the same development even to a greater degree, on account of the rapid growth of the very long hypocotyl, but a quite different condition was found, different even from that found by Warming for our species, *R. mangle*.

The inner rounded end of the embryo is connected with the integument by a well-developed "Saugorgan" structure consisting of cells of several layers, with thin walls and rather elongated in outline, the upper layer of which is supplied with warts and papillæ, which apparently transfer food to the embryo. But the endosperm cells around the cotyledonary collar region have large thin-walled watery cells, among which the absorptive papillæ are more numerous. Haberlandt shows this in a series of excellent figures (l. c., Pl. XI.), but that these papillæ merely function as, or are absorptive organs, Haberlandt does not concede. His conclusion is that this tissue is an enzyme-secreting layer of cells which perhaps secretes diastase, and to prove this he placed starch grains on these papillæ and learned that in twenty-four hours the grains on the rounded head region were deeply corroded, while those of the collar were less so. The large watery cells of the latter region Haberlandt regards as water reservoirs for the delicate absorptive tissue of the "head" region. This he regards as a special adaptation to the physiologically dry habitat of the mangrove and a protection against transpiration.[91]

In the more recent work of Cook there is also mentioned (l. c., p. 273) the fact that the cells of the integument are much denser

[91] Haberlandt, G., loc. cit., p. 105.

than those of the endosperm and that the union between the two layers of cells is very close. Cook further has divided the periods of growth of the embryo into three definite periods; first, the first growth of the cotyledons, during which they enlarge and are the means of storing up the food for the later growth; second, the cotyledons almost cease growing, while the hypocotyl elongates and the plumule is forming, and the beginnings of vascular elements take shape; third, the second growth of the cotyledonary body which pushed out the region of union of the cotyledons and the hypocotyl so that the cotyledonary body projects like a green collar beyond the apex of the fruit. An absciss layer is then formed at the base of the plumule and the hypocotyl drops off.

## Polyembryony.

The presence of four ovules in the young condition of the fruit and the habitual development of only one of these into a seed naturally leads the investigator to look for polyembryony in the genus. This condition actually does happen at rare intervals and has been noted by a few observers. Warming quotes Piso,[92] who figures this rare phenomenon of two or more radicles pushing out from one fruit. Baron Eggers[93] is also quoted as estimating from his observations on this species in the West Indies that polyembryony occurs three times in one thousand cases and Du Petit Thouars[94] is also reported to have observed this. Polyembryony may occur according to the wide usage of the term by some botanists, *i. e.,* two or more embryos may develop within one embryo sac by the formation of several embryos, one of which originates from the egg and it is this which Warming figures in Pl. VII.–VIII., or in the wider sense of two or more ovules germinating from one fruit. The difference may easily be seen on cutting away the fruit wall; if only one seed is present, it can only be interpreted as true polyembryony. In the second case two or more seeds would be noticed.

[92] Piso, G., loc. cit.

[93] Eggers, H., loc. cit., p. 180.

[94] Thouars, Albert du Petit, "Notice sur le Manglier," Desvaux's *Journal de Botanique,* t. 3, p. 27, 1813.

More recently Guppy has observed cases of polyembryony, but all of the cases which he observed seem to be of the second type, in which more than one seed germinated. This naturalist counted eight hundred fruits on trees of *R. mangle* in Fiji and found only nine cases of polyembryony, eight with two radicles protruding and one with three. In particular localities he found as many as two or three per cent. of the fruit showing polyembryony. Perhaps this indicates an hereditary factor and tendency in certain trees of a region for evolution to a condition of maturing and germinating all four of the ovules in a fruit. No cases of polyembryony seem to be reported for other species than *R. mangle.*

## Embryonal Development.

The length of time required for the complete development of the embryo from the time of fertilization until the fall of the seedling has been estimated by some observers and actually recorded exactly by a few who pollinated the flowers. Even in Jacquin's time[95] it was recognized that it was a long and slow process, for he remarks that the time is twelve months to the dropping of the seedlings, and that it takes three months for the hypocotyl to appear at the top of the fruit.

While an opportunity was not given to observe this for *R. mangle* by the writer on account of the brevity of the laboratory season at Tortugas, some idea was gained of the relative rate of growth by marking the hypocotyl of very young seedlings with bands of India ink and measuring the distance of the ring from the apex of the fruit, as well as the spaces between other rings on the length of hypocotyl, after a period of a few weeks, June 11 to July 15. On the former date about 20 hypocotyls were marked in the above described manner with rings one centimeter apart. At the end of the time on July 15, during a return trip to Key West and Stock Island, where the trees were growing, it was found that twelve of the seedlings were still on the trees and had made various growths, viz., 5, 3, 5, 3, 6, 5, 3, 6, 5, 4, 5, 3 centimeters, or approximately 4.7 centimeters, growth in the thirty-four days which had elapsed.

[95] Jacquin, N. J., "Selectarum Stirpium Americanorum," 1763, p. 141.

A great deal of work has been done by Guppy[96] on plant dispersal and in one work he has devoted several chapters to the mangrove and on page 451 of the above book gives the "history of the reproductive process in *Rhizophora* from the fertilization of the ovule to the falling of the plantlet or seedling from the tree." He goes on to say: "I devoted great attention to this subject in the instance of *Rhizophora mangle,* being desirous of determining two points, in the first place as to whether there was any period of rest between the maturation and germination of the seed, and in the second place as to the period that elapsed between the commencement of germination and the fall of the seedling." "The principal change in the ovary for the first three or four weeks after fertilization is shown in its increased breadth. The increase in height is but slight during this period; and in fact after thirty days the ovary only added two millimeters to its original height of three millimeters. After this the growth of the fruit proceeds until the tip of the radicle pierces its summit, the fruit being then about eleven lines (2.8 cm.) long. *From the date of fertilization to the time the radicle pierces the top of the fruit a period of about fifteen weeks elapses.* (The fruit, it should be here remarked, continues to grow in length and breadth after the radicle has protruded, attaining a length of thirteen or fourteen lines (3.5 cm.) when the seedling or 'keimling' is ready to fall.)"

"It will be observed that there is no period of rest in the growth of the fruit up to the date of the protrusion of the radicle. It may also be shown that there is normally no pause between the epoch of the maturation of the seed and the beginning of germination or, in other words, that from the time of the fertilization of the ovule to the onset of germination there is no cessation in the process of growth of the embryo. That period of dormant vitality which almost all seeds pass through forms no normal feature in the life-history of this species of *Rhizophora.*"

In Guppy's more recent work[97] of 1917 in the West Indies and the Azores he gives a summary likewise of the period which elapses

[96] Guppy, H. B., "Observations of a Naturalist in the Pacific," Vol. II., 1906.

[97] Guppy, H. B., "Plants, Seeds and Currents in the West Indies and Azores," London, 1917.

between fertilization and the fall of the seedlings of the species in the former region and states it to be nine or ten months.

Before leaving this subject of morphology and histology, there are two anatomical features which deserve special mention and which occur in nearly every tissue of *Rhizophora*. These two peculiarities are the indioblasts or trichoblasts and the tannin cells. The trichoblasts were, according to Warming, perhaps first described by Decaisne,[98] who remarked their presence in a "root." They are perhaps better seen, however, in a hypocotyl, which if broken transversely the surface of the fracture is seen to be densely bristled with the tips of the thousands of idioblasts embedded in the intercellular spaces of the cortex, as well as the medulla and even vascular region (Fig. 2, Pl. V.). The most of the idioblasts in this organ, as well as those in stem and roots, are composed of four elongated and taper pointed branches joined in the middle by a short connection, the whole structure appearing as a letter *H* (Fig. 2, Pl. IV.). The idioblasts of the leaves, however, are more irregular and branched or even stellate in form with the branches ramifying among the cells. Sections of this type are seen in Fig. 1, Pl. V. In the older and more lignified tissues, as the stem and also in the hard calyx and ovary, the idioblasts more nearly resemble the stone cells of fruit pits and of the leaves of *Camellia* and *Osmanthus*, having the lumen almost entirely filled up. These structures, as Warming remarks, very soon render a razor entirely unfit for use in the preparation of histological material. The same author regards the function of the structures as mechanical in preventing shrinking and shriveling of tissues when exposed to the great heat of the sun. But as they are frequent also in parts which are not so exposed, as for instance the absorptive roots and the interior of the fruit and flower, etc., this theory of support against shrinkage due to heat is not necessarily true, but it may be conceded that their rôle is mechanical and they do support the large intercellular spaces found in some of the tissues. In discussing fibers and hairs, De Bary[99] says: "There occur in phanerogams fibers which are freely and

[98] Decaisne, J., *Annales des Sciences Naturelles,* 2, Series 4, p. 76, 1835.

[99] De Bary, A., "A Comparative Anatomy of the Vegetative Organs of the Phanerogams and Ferns," tr. Bower and Scott, pp. 130 and 220, 1884.

often abundantly branched and of a form which varies according to the special place of their occurrence. These usually occur in dissimilar lacunar tissue with their branches pushed into its interstices. In as much as these project like many-branched hairs into wide air-containing spaces (as *Rhizophora*) . . . and also occur in many tough leathery foliage leaves . . . they appear to serve as a strengthening apparatus for the tissue. De Bary further mentions their occurrence in the pith and cortex of *Rhizophora* (p. 220) but has overlooked them in other parts. He regards them as being closely related to sclerenchyma fibers and only differ from them in shape and distribution.

The tannin cells do not seem to have received so much attention from histologists as the idioblasts. Most investigators on *Rhizophora* have mentioned the occurrence of tannic acid in large quantities, but few have remarked on the localization of this substance. The large cells of the root-cortex, both of the aërial prop-roots and to some extent of the absorptive roots, are filled with large, rather polygonal cells, which contain tannin. The tannin in the cells appears as tiny brown granular masses, which stain a dense black when special preparations are made of tissues stained with copper acetate or ferric chloride. The pericycle region of the soft absorptive roots contains the most in the subterranean roots which perhaps have the least of any organ in the plant. In the leaves, as seen in Fig. 4, Pl. IV., the large special tannin cells are the first two layers of the hypodermis, just beneath the epidermis. The pericarp of the fruit and even the young embryo also show notable qualities of tannin in specially prepared material. The rôle played by tannin in the economy of *Rhizophora* will be discussed in the next chapter. The largest amount is found in the cortex of the stems and aërial roots.

## Physiology.

The physiological relation of *Rhizophora* to its various media of growth is perhaps the main subject of consideration in this paper. The idea of work on the physiology, as expressed by transpiration and absorption, had its inception in the interest aroused by the apparent ability of these trees to grow almost equally well in either fresh or salt water. The transpiration as affected by the climate was not of paramount interest, as that has received much attention by such investigators in warm climates as Haberlandt,[100] Holtermann,[101] Giltay,[102] Wiesner,[103] Unger,[104] Stahl[105] and many others. As mentioned before, the *Rhizophora* trees grow along the shores of bays and the mouths of rivers, where the above conditions are found, so an attempt was made to study the effect of this environment as evidenced by the transpiration rates of plants in similar, but controlled conditions. At the same time various soils were experimented with.

Seedlings of the first or second year's growth were secured at Cayo Agua, one of the lower Florida keys, and brought to the Tortugas Laboratory on the laboratory yacht, a distance of about ninety miles. The seedlings were found in natural beds under the parent trees along the shores of this island. During the transit some of the seedlings died, but enough were saved to start several hundred cultures. These cultures were made in large heavy glass beakers about ten inches in diameter.

These seedlings were placed in a jar, in soil and mud, etc., according to the kind of culture, and the jars filled up with water. The water was of a definitely known concentration of sea water or pure rain water from the laboratory cisterns. The soils ordinarily used were either the native Tortugas sand, a very coarse calcareous sand composed of the remains of calcareous algæ, corals, echinoderms, gastropods, etc., or a reddish soil brought down to the laboratory from the vicinity of Maplewood, N. J. This latter soil appeared to be composed of a disintegrated, ferruginous sandstone.

[100] Haberlandt, G., "Ueber die Groesse der Transpiration im feuchtem Tropenklima," *Ebenda,* Bd. XXXI., 1898.

[101] Holtermann, K., "Die Transpiration der Pflanzen in den Tropen," *Sitzb. der kgl. preuss. akad. des Wissen. Berlin,* Bd. XXX., 1902.

[102] Giltay, E., "Die Transpiration in den Tropen und in Mitteleuropa," II., *Ebenda,* Bd. XXXII., 1898.

[103] Wiesner, J., and Pacher, J., "Ueber die Transpiration entlaubter Zweige," *Oesterr. Botan. Zeitschr.,* Wien, Bd. XXV., 1875, p. 145.

[104] Unger, F., "Neue Untersuchungen ueber die Transpiration der Pflanzen," *Ebenda,* Bd. XLIV., 1862.

[105] Stahl, E., "Einige Versuche ueber Transpiration und Assimilation," *Botan. Zeitung,* Bd. LII., 1894, p. 117.

A few cultures were also potted in a dark, bluish, gray mud taken up from the bottom of the moat at Fort Jefferson on the adjacent Garden Key. This mud, which seems very similar to that of typical mangrove swamps, gets its dark color from decaying organic matter in it and is also heavily charged with hydrogen sulphide arising from the decomposition, just as is the ordinary mangrove swamp mud.

Some of this mud was boiled to drive off the gas and other cultures were made of the unboiled mud to learn if there might be a difference in the rate of transpiration.

The water concentrations used in the soil experiments were pure salt water and 50 per cent. salt water.

## Technique.

The methods of getting at the rate of transpiration which seemed the most feasible considering the available supply of material was that of Stahl. This method, while only a colorimetric method and hence not recognized as so exact as are perhaps volumetric methods, gave very interesting results with a few modifications to suit the conditions obtaining in the laboratory. A Ganong leaf-clasp was used for the transpirometer. The indicators for this little instrument are discs of Swedish filter paper saturated in 4 per cent. cobaltous chloride solution. These disc are inserted in the rings inside the thin glass sides of the instrument which is then clamped on a rod stand and the apparatus placed beside a culture jar. Full-grown leaves of about the same size on plants of the same age were used for tests. A small difficulty was encountered in the high humidity content of an island and tropical climate atmosphere, since the indicator discs necessarily had to be absolutely dry. This difficulty was overcome by keeping the discs in a calcium chloride desiccator of large size which conveniently held the whole instrument with its ball-and-socket adjustable arm. In making tests, the paper discs were placed in the clasp and dried over an alcohol flame until the characteristic pink color of the paper at ordinary atmospheric conditions was replaced by a deep blue of absolute dryness. The whole clasp was then quickly placed in the desiccator, which was cooled artificially by an ice chamber about it. This was found necessary to expedite the taking of tests, as the heat absorbed by the apparatus during the drying had a vitiating effect on the transpiration experiment unless cooled, and if allowed to cool to the room temperature slowly, too much time was lost between tests. After a minute or two, the apparatus, sufficiently cooled and dry, was quickly removed from the desiccator and clamped on the upright rod support beside the culture jar, the selected leaf placed in the clasp and the screws slightly adjusted to press the sides of the clasp on the surfaces. By a stop watch the time was then noted that was required to change the color of the indicator disc to a uniform pink, due to the effect of the moisture transpired through the stomata and epidermis of the leaf. As there are no stomata on the upper surface the change in color for the disc on the upper side of the leaf always lagged in the time interval from 65 to 80 seconds behind the lower or stomatal side. This interval was constant for nearly all tests and for this reason only the lower-side indicator was used for the records. An error in calculating the time interval required to effect the change in the indicator occurs in the loss of time required to adjust the instrument on the plant, during which the atmosphere has an opportunity, for a few seconds, to get in its influence on the instrument, but the transfer from the desiccator to the plant becomes routine after a few hundred tests and this time error of a few seconds may be disregarded, as it is constant for all the tests.

The successive tests were made at one time on each culture jar, separate leaves, one each, of the three plants in the jar being used. The time of taking the tests was as far as possible made in the middle portion of the day and every effort was made to avoid jarring or shocking the plants just before or during a test, on account of the accelerating effect of shock on the transpiration rate. The records were all marked in notebooks and the average taken for the three tests on one culture jar.

The cultures were kept on large tables holding about thirty jars in the laboratory, which was open on all sides and contained ventilator trap doors in the roof which were propped open during the day. The plants were thus sheltered from the direct rays of the sun and rain. However, during the long, still, calm days of June and July there is very little atmospheric variation in the Tortugas climate. The greater part of these two months is made up of clear, sunny days with almost no wind. The average wind velocity for the region, according to the U. S. Weather Bureau Records from Key West, is 9.6 miles per hour for the year, but most of the gales occur in the fall and winter months, September and October being called the "hurricane months."

The average temperature for the year is 76.8° F. with a maximum of 88° F. and a minimum of 77° F. during the months in which these tests were made, while the average relative humidity for the whole general region is about 73 per cent.

In both the soil and the water concentration series of experiments it was found advisable to siphon off the water from each culture jar daily. In doing this, two objects were attained—a fresh supply of water containing the various gases, etc., in solution was furnished the roots of the plants, simulating the tidal action of the sea in the natural beds in the mangrove swamps and also by this means the mosquito larva were removed to a large extent, the cultures of plants in fresh water and the higher dilutions of salt water being an ideal place for the breeding of mosquitos if left undisturbed.

In the water concentration series of cultures several hundred seedlings were potted in the jars similar to the above described soil experiment cultures. The soil used however to anchor the seedlings was uniform for all the series, that is, only the Tortugas shell sand was used.

The water concentrations employed for the series were as follows:

Series *A*—100 per cent. fresh water.
Series *B*— 75 per cent. fresh water.
Series *C*— 50 per cent. fresh water.
Series *D*— 20 per cent. fresh water.
Series *E*— 10 per cent. fresh water.
Series *F*— 5 per cent. fresh water.
Series *G*—100 per cent. salt water.

In 1915 a series of cultures was made on hyperconcentrated sea water of 140 per cent. concentration. The transpiration rate records for the culture showed a very slow rate of transpiration and in fact the whole metabolism of the plants was so retarded that the plants slowly yellowed, dropped the leaves and died after a few weeks. The rate on the basis of Stahl's method was 5.66, *i. e.,* approximately there was required 5.66 minutes to change the indicator of the transpirometer.

In addition to the cultures in water, there was a series planted in shell sand and merely kept moist with salt water, but also kept in the laboratory sheltered from the direct rays of the sun, wind and rain. Another series, however, was placed in boxes of sand, merely kept moist but placed on the landing dock of the laboratory in full glare of sun, etc. This situation most nearly approached the living conditions of *Rhizophora* seedlings drifted up on the beaches of the Tortugas Islands. As there are no mangroves in these islands except two young trees in a very sheltered position on Garden Key, an inquiry into the physiological behavior of these drifted plants was attempted to learn why the mangrove does not survive in this group. This subject will be discussed in the light of the above experiments in the chapter on ecology. However, it suffices to say here that the hard conditions of these cultures proved too much for the seedlings and one pair of tiny leaves would unfold after another with very short internodes and each pair would successively be burned up by the intensely hot sun and the glare of the reflection of the white sand in which they were planted together with the greatly reduced absorption from the merely moist, coarse, porous substratum. After a month of this heroic attempt at growth, the seedlings succumbed when the reserve food in the hypocotyl was exhausted, no foliage being put forth during their brief existence that attained sufficient size on which to take transpiration rate records.

In a previous season at Tortugas a number of cultures was made of seedlings planted in jars of the Fort Jefferson moat mud, but the water was not siphoned from these cultures daily and a fresh supply put on, so that in a short while the water became so charged with $H_2S$ gas that it produced a toxic effect on the plants, from which they soon died. This toxic effect of the hydrogen sulphide gas was of course due to the higher concentration of the acid solution, the ionization being H + and HS —. In cultures of which the mud had been previously boiled to drive off the gas, the ultimate death of the plant was only postponed as the further decomposition of the organic substances in the mud soon produced enough $H_2S$ to again render the culture toxic. It is presumed that the constant action of the waves and the daily tides so dilute the gas in the natural mangrove beds that the toxicity is removed. Many factors enter into this question, as the precipitation of sulphides by the inter-action of bases in the sea water, action of the products of denitrifying basteria in large quantity in the tropical waters and other complex chemical phenomena. On account of the early death of the plants no records could be made of these cultures, or at least in sufficient number to warrant any definite conclusions. All the cultures were allowed about three weeks to adjust themselves to the changed conditions in the laboratory from those of their natural beds, before any records were taken. By this adjusting process time was also given to eliminate any seedlings which were not healthy or showed signs of not reacting normally.

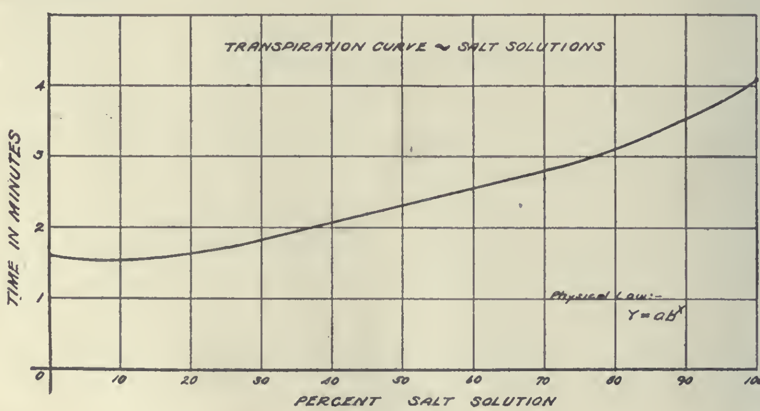
Lastly a series of two hundred young trees was planted on a small mound of mud in the moat at Fort Jefferson during the summer of 1915. The top of this little mound of debris was only moistened at the highest tide and this exposed part was largely composed of coarse broken corals and shells, pieces ten to fifteen centimeters in dimension. The little plants about one half meter high were set at varying levels on the mound, some on top in the dry coarse debris and the lowest almost submerged even at low tide. In 1916 on the writer's return to Tortugas only twelve of these trees were alive, the winter storms had so disturbed the mound that many were washed away, the remaining ones were growing and apparently in good condition. The significance of the experiment will be considered under the ecological relations.

## Transpiration Records.

The result of about two thousand records made in both seasons of the years 1915 and 1916 are now set forth. The intervals between the stop-watch registrations were all calculated for each test, in minutes and fractions of minutes, and these intervals then averaged for each set of three tests on a culture, and then general averages made of the series and finally all the sets of records made at different times on each series were averaged for each series. These final averages, as expressed for each series, are as follows, in the Water Concentration Class of experiments.

Series *A*—100 per cent. Fresh—1.6 minutes.
Series *B*— 75 per cent. Fresh—1.7 minutes.
Series *C*— 50 per cent. Fresh—2.4 minutes.
Series *D*— 20 per cent. Fresh—2.8 minutes.
Series *E*— 10 per cent. Fresh—3.2 minutes.
Series *F*— 05 per cent. Fresh—3.9 minutes.
Series *G*—100 per cent. Salt —4.1 minutes.

By arranging the data in curves, a graphic idea may be gained of the rates of transpiration of these plants in their various concentration cultures, and by applying certain mathematical formulæ definite laws may be deduced for the phenomena. In a preliminary report on the work[106] before the data were all tabulated a formula was used with almost the same result as that given in the following curve.




Graph No. 1.

But a better formula appears to be the one here given $y = ab^x$. In the curve the time intervals in minutes are arranged as ordinates

[106] Bowman, H. H. M., "Physiological Studies on *Rhizophora*," *Proc. Nat. Acad. Sciences,* Vol. 2, No. 12, Dec., 1916, p. 685–688.

and the concentration percentages as abscissæ. That is, the curve indicates the period of time required by the plants to transpire equal quantities of moisture when planted in varying concentrations of water. When growing in fresh water, the plant transpires the unit quantity of moisture in 1.6 minutes, when growing in 100 per cent. salt water, to transpire the same quantity there is required 4.1 minutes. The effect then of increasing the salt content is to retard the time of equal transpirations of moisture. The physical law expressing this progressive increase of time interval, necessitated by the increasing concentration, has the mathematical form $y = ab^x$. That is the time, $y$, for a plant to transpire a unit quantity of moisture when the percentage of salt solution is $x$, is equal to constant $b$ (approx. $= z$) multiplied by a constant, $b$ (approx. $= 1.79$), raised to $x$ power. For the percentage concentrations used in this work the rate of transpiration then varies directly with the concentration.

The result of these experiments can only in a general way be compared with those of other workers on transpiration, because there are too many factors which were necessarily quite different in the materials and methods. The plants themselves are specially adapted to a water environment and protected against an excessive transpiration, while the ordinarily high salt concentration of the medium of growth makes absorption difficult. The rather high humidity of the air tends to reduce transpiration, while the heat and intense light of their habitat helps to increase it. The general results, however, do correspond with the experiments of Ricome[107] on plants of *Malcomia maritima* and *Alyssum maritimum*. This investigator cultivated the plants in normal soil and salty soil and transferred to plain Knop's nutrient solution and in Knop's solution to which one per cent. of salt (NaCl) was added. While the general temperatures and humidity were not the same, the light intensity was rather diffuse as in the present studies, but the methods of measuring the transpiration differed. Ricome found that both the absorption and transpiration were less in the plants grown in

[107] Ricome, H., "Influence du Chlorure de Sodium sur la Transpiration et l'Absorption de l'Eau chez les Vegetaux," *Comptes Rendus de l'Acad. des Sci. Paris*, T. CXXXVII., 1903.

salt soil than in the sodium chloride free soil and likewise for the Knop solution cultures. He finds that NaCl externally makes absorption through the roots difficult and that contained in the plant's tissues lessens transpiration. Other workers have also experimented with plants in solutions of different salts, as Burgerstein,[108] who grew plants in borax solutions of one to three tenths per cent. concentration and by comparison of the transpiration of similar plants in distilled water, he found that those in the borax solution transpired much less, but an objectionable feature in those experiments was the highly toxic effect of boric acid and borates, as Peligot[109] has shown, since the plants began to droop and die on the second day of the experiments.

Cuboni[110] who experimented with sprinkling branches of various trees and shrubs with thin solutions of calcium hydroxide and measuring the transpiration by photometric methods found that this substance had no effect, but as there was no absorption here the results cannot be compared. The available water for absorption is naturally the factor most concerned in transpiration and as the increasing density of the solutions makes osmosis and absorption more difficult the corresponding phenomenon is decreased in amount. Not all salts in solution however have this physical effect, if the works of Sachs[111] and Senebier[112] may be considered. The effect is also partly chemical, and the physical osmotic relations cannot be supposed to be due to the density of the solutions alone, thus Senebier, who was an earlier investigator on the subject, states that aqueous solutions of sodium sulphate, potassium nitrate and potassium tartrate occasion an acceleration in the water movement in plants, while Sachs claims a retardation for ammonium sulphate and sodium chloride. Both the experimenters worked with twigs and so the action by root absorption is not considered and the assump-

[108] Burgerstein, A., "Die Transpiration der Pflanzen," p. 146, 1904.

[109] Peligot, M., *Comptes Rendus de l'Acad. des Sci. Paris,* t. 83.

[110] Cuboni, G., "La Transpirazione e l'Assimilazione nella Foglie trattata con Latte di Calci, Malpighia," Vol. 1, p. 295, 1887.

[111] Sachs, J., "Ueber den Einfluss der chemischen und physikalischen Beschaffenheit des Bodens auf die Transpiration der Pflanzen. Landw. Vers-Stationen," Bd. I., 1859, p. 203.

[112] Senebier, J., "Physiologie Vegetal," Geneve, 1800.

tion may be made that the effects were more chemical than physical and so according to Sachs it would seem that sodium chloride has a retarding chemical effect in addition to the retardation of its physiological action in the osmosis of root absorption. However, as Burgerstein says (p. 152), neither investigator carried on a large series of experiments and Senebier moreover was only concerned with the amount of water as indicated by the absorption.

In connection with measuring transpiration of plants in various concentrations of salts as the series in this paper, Burgerstein[113] has made a series of interesting measurements, partly with woody twigs and partly with rooted seedlings in 0.10 to 1.0 per cent. solutions of the following nutrient salts: potassium, calcium and ammonium nitrates, magnesium and ammonium sulphates, potassium phosphate and potassium carbonate. In very dilute solution, .05 to 2.5 per cent., the transpiration, when compared with that of plants in distilled water, is increased, the higher the concentration of the solution is increased, until at a definite concentration a maximum is reached. For the corn plant (*Zea mays*) this is about 2.5 per cent. A further interesting feature of Burgerstein's work is that this maximum transpiration-concentration is lower for the alkaline salt solutions and higher for the acid reacting salts than for the maximum point of nutrient salts with a neutral reaction. In solutions above this degree of concentration the transpiration steadily declined, so that a general rule could be deduced that in .3 to .5 per cent. solutions the transpiration was already less than that of plants in distilled water.

As most of the cultures of the mangroves used in the experiments described in the present paper were grown in much higher concentrations than those of Burgerstein, the optimum concentration of very dilute solutions could not have been detected, or its climax of transpiration increase observed. However, in the curve No. 1 there is seen a slight sag as the percentage increases from fresh water toward the 10 per cent. solution. This may be interpreted as the slight increase in transpiration (here expressed in time rate)

[113] Burgerstein, A., "Untersuchungen ueber die Beziehungen der Nährstoffe zur Transpiration der Pflanzen. I. Reihe," *Sitzb. der kais. Akad. der Wiss. in Wien,* Bd. LXXXIII., p. 191, 1876.

due to the dilute solution, before the optimum concentration is reached, after which it showed a steady decrease in transpiration, or as here expressed in an increase in the time interval. In addition to these results as found by Burgerstein, Sorauer[114] noticed that in cultures kept in solutions of concentrations above this optimum or maximum point, not only was the transpiration decreased but the production of dry substance in the plants as well. The whole result of the series of experiments may be said to consist in showing the transpiration relation of the mangroves growing in solutions, as plants specially adapted to such halophytic aquatic conditions, that for increases of salt concentration in their media of growth there is a corresponding definite retardation of the transpiration rate which may be expressed in a mathematical formula.

## Transpiration of Soil Cultures.

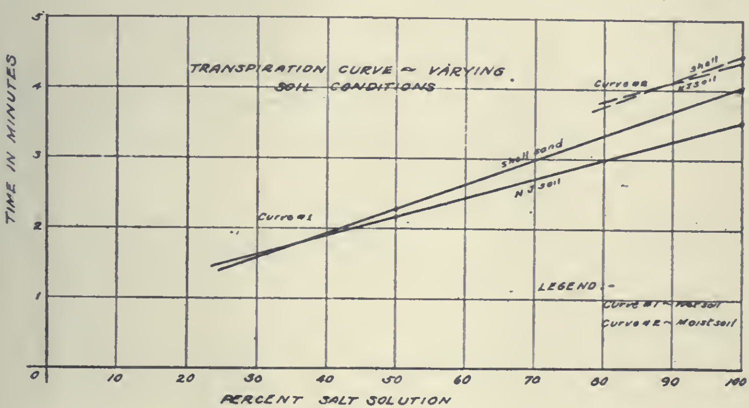
The second series of cultures as outlined under the description of the methods of handling the material is the series of soil experiments. The two soils above mentioned were used and two conditions of soil moisture content employed, *i. e.,* plants in boxes of soil merely moistened with water, and plants in jars kept flooded with water. The method of taking the records and the laboratory conditions as to light intensity, atmospheric humidity and temperature were the same as for the previous experiments, as was also the procedure of siphoning off the water from the jars and renewing the water daily to keep down the mosquito larvæ.

The factors entering into this series of experiments are really much more complex than those in the first set of cultures as that involved only the salt concentration of the water, the soil (shell sand) used to anchor the plants being in all the cultures the same. But with the use of two soils, the one of a complex chemical nature (New Jersey soil), and the two sets of soil moisture contents, the problem is more complicated. The results of the experiments are set forth in Graph No. 2.

The influences on the transpiration are here due perhaps more to the chemical action of elements in the solution than to physiolog-

[114] Sorauer, P., "Studien ueber Verdunstung, Forsch. an der Gebiet der Agrikultur-Physik von Wollny," Bd. III., 1880, p. 351.

ical effects of varying concentrations. As will be noticed the above graph shows two double curves—No. 1 for the flooded soil and No. 2 for the soil merely moistened. An interesting feature of the two curves considered together is that there is illustrated very clearly the relation of transpiration to soil moisture content. Stenström[115] expressed this relation in a principle which shows the connection




Graph No. 2.

between the soil moisture content, the atmospheric humidity and the transpiration of plants thus. $\frac{S.M.}{H} = T$, in which equation the letters stand for the above factors in the order named. Many physiologists have shown the relation between available water and transpiration and notable among these is Aloi,[116] whom Burgerstein quotes (p. 137, l. c., Bibl., 107) as showing that with a normal moisture content the transpiration was less than that of plants in a saturated soil. "Ueber den Einfluss der Bodenfeuchtigkeit auf die Wasserabgabe der Pflanzen stellte auch Aloi viele Versuche an, welche lehrten dass die Transpiration bei einer 'umidita normale' geringer war als in einem 'terreno molto umido.'"

[115] Stenström, K., "Ueber das Vorkommer derselben Arten in verschiedenen Klimaten an verichiedenen Standorten mit besonderer Berucksichtigung der Xerophil ausgebildeten Pflanzen," *Flora*, Bd. LXXX., p. 117, 1895.

[116] Aloi, A., "Influenza dell' Umidita del suolo sulla Transpiratione delle Piante Terrestri," *Atti dell' Acad. Gioenia di Science Nat. Catania*, Ser. 4, Tome VII., 1894.

Curve No. 2, showing the moist soil transpiration, is very short and unfortunately only about two hundred records were made on this series of cultures. The same characteristics are shown for both curves and the lines are parallel. The two sets considered together show clearly that the rate of transpiration depends upon the amount of moisture in the soil available for absorption by the roots.

Curve No. 1 shows three things—first that mangrove seedlings planted in dilutions over 35 per cent. salt transpire more rapidly when planted in New Jersey soil than in shell sand. Second, that similar seedlings under the same conditions in dilutions of 35 per cent. salt water transpire at the same rate when planted in either soil and third, similar seedlings planted in water less than 35 per cent. salt water transpire more rapidly when growing in shell sand. These three facts can only be explained by the chemical action of constituents of the soils reacting with those of the water. The balance of solution for these constituents is evidently reached at a concentration of about 35 per cent. salt water in the cultures indicated by curve No. 1, while the same condition of chemical equilibrium is apparently reached at a concentration of 88.5 per cent. salt water in the cultures of plants in merely moistened soil. While it is not known what the chemical constituents of the soils are, the water has been very carefully analyzed by the chemist of the U. S. Geological Survey for the Laboratory Director, Dr. A. G. Mayer.[117]

The explanation of the interaction of the chemical constituents of these two soils with the elements of the salt water in the varying concentrations used in these experiments is really a complex problem to be taken up by the chemist and physicist. However, it may be suggested with propriety here in a paper dealing with more purely botanical phases that the above interaction of the various elements in the soils and salt water during ionization in the solutions proceeds along the general action shown in the addition of chemicals to sea-water, discussed in a recent paper by Haas.[118] In this work by

[117] Mayer, A. G., Annual Report of the Director of the Dept. of Marine Biology, *Carnegie Inst. of Washington, Year Book* for 1910, p. 122.

[118] Haas, A. R., "The Effects of the Addition of Alkali to Sea-Water upon the Hydrogen Ion Concentration," *Jour. of Biol. Chem.*, Vol. XXVI., No. 2, Sept., 1916, p. 515.

Haas, strong sodium hydroxide solution (2.4813 N) was added to sea water in small amounts and titrated by means of the gas chain and the results given in a curve (p. 517) and in explanation of this curve, the investigator says: "The titration curve shows that on adding alkali to sea water the hydroxyl ion concentration at first rises rapidly and then very slowly until the magnesium hydrate has all been precipitated. After this further additions of alkali cause a more rapid rise in the concentration of the hydroxyl ion, but this rise is soon checked by the precipitation of calcium hydroxide. After the calcium hydroxide is all precipitated further addition of alkali will cause a corresponding increase in the concentration of the hydroxyl ion."

While we are not in this paper concerned primarily with the concentration of the hydroxyl ion, the formation of the successive precipitations proves very interesting and it is phenomena of this sort which very likely cause the transpiration of the seedlings to go on more actively in dilutions over 35 per cent. salt water when planted in New Jersey soil and also to accelerate the transpiration when planted in Tortugas shell sand in concentration less than 35 per cent. salt water. This latter group of results may be logically explained by the hypothesis that with the atmospheric humidity and temperature conditions the same, the transpiration would be accelerated in the less highly concentrated solution, according to the general law of transpiration, since the relatively pure calcium carbonate composition of the shell sand is less soluble than the more complex New Jersey soil. It is also less finely comminuted than the latter soil and as Reed[119] has shown in the transpiration of wheat seedlings that calcium carbonate added in small amounts to water cultures or soil cultures has an accelerating effect, then also the dilution of the sea water being less than 35 per cent. there are smaller amounts of salt in it, so that on the whole the behavior in regard to transpiration of these cultures is normal for the conditions.

The acceleration, however, of the rate of transpiration of cultures in New Jersey soil and concentrations over 35 per cent. salt

[119] Reed, H. S., "The Effect of Certain Chemical Agents upon the Transpiration and Growth of Wheat Seedlings," *Bot. Gaz.*, Vol. XLIX., 1910, p. 81.

water must be the manifestation of some such principle demonstrated by Haas's experiments.

## The Physiology of the Prop Roots.

A small series of experiments was made at Miami, Fla., on the transpiration through the lenticels of the pneumatophore or prop roots of older *Rhizophora* trees. Some of these trees were growing along the shores of Biscayne Bay and some along the banks of the Miami River. The salt concentration of the bay is not as high as the ocean outside, due to the effect of the streams which empty into it and the river, of course, is approximately fresh water; however, the tide produces a noticeable effect in the river and for the comparatively short distance up the river that the mangroves extend there is perhaps a commingling of the fresh water of the river and the salt of the tide; however, the densities of both the bay and the river were measured with the hydrometer and the measurements will be discussed under the ecology.

Essentially the same technique was employed in taking these prop root transpiration records as that used for the leaf records made at Tortugas. The leaf clasp naturally could not be used conveniently for taking records from the roots, which are cylindrical in shape and of varying thicknesses. To overcome the difficulty of adjusting the transpirometer to this cylindrical surface a modified transpirometer was devised by the writer and made for him by a firm of instrument makers. This device consists of two curved glass sides held in a curved metal frame which is constructed with two grooves along the upper and lower edges respectively. Into these grooves the edges of the indicator paper is slipped and held in place inside the curved glass surfaces. The two curved glass sides are held together on one side by a neat but strong spring, which opens the instrument and permits its being clasped about a root when the two discs of hard rubber are pressed together behind the spring. The indicator paper was inserted and dried over the flame and put into the calcium chloride desiccator. When cool the instrument was adjusted to the root and the record taken. As no control could be had over the concentration of the substratum and water concentration in which these old trees were growing, the results here given merely illustrate the fact that these aërating or prop roots actually do transpire water vapor and that there is a perceptible difference in the rates of transpiration of trees growing in the comparatively fresh water of the river and those in the more highly concentrated salt water of the bay. The average for the series of river tests was 2.37 minutes required to change the indicator in the modified transpirometer, while the bay tests average was 3.66 minutes.

These prop roots are really aërating roots as Karsten[120] and Schimper[121] and others have shown in their experiments on other trees of the mangrove habit. In the activity of gas exchange as performed by aërating roots, there is, of course, considerable moisture transpired. This function of aëration of roots is well discussed by Karsten for the prop roots of *Bruguiera eriopetala* on experiments which he conducted at the Buitenzorg Botanical Garden. These experiments were very elaborate and were done in the field, for which a cement base had to be constructed in the mud of the swamp and bell jars and glass apparatus fitted on the roots *in situ*. Manometers were used to regulate pressure and the amounts of $CO_2$ exchanged in respiration were measured by precipitating it with barium hydroxide as barium carbonate and then back-titrating it with oxalic acid and phenolphthalein. These experiments established the fact that the roots do function as respiratory organs for definite areas of the plant body and regulate the air supply for these trees whose roots are sunk in the poorly oxygenated and water-saturated mud and slime of the swamp, and they also help to regulate the fluctuating conditions produced by the tides when part of the tree is submerged, and at other times exposed. Similar experiments and observations by Goebel[122-123] on *Sonneratia acida* and *Avicennia officinalis*, and by Schenck[124] on *Avicennia tomentosa* and

[120] Karsten, G., loc. cit., p. 41.

[121] Schimper, A. F. W., "Botanische Mittheilungen aus dem Tropen," Heft 3, Die Indo-malayische Strandflora, 1891, p. 37.

[122] Goebel, K., "Ueber die Luftwurzelne von Sonneratia," *Ber. der Deut. Bot. Gesell.*, IV., p. 249.

[123] Goebel, K., "Pflanzenbiologische Schilderungen, I. Südasiatische Strandvegetation," p. 113.

[124] Schenck, H., "Ueber Luftwurzeln von *Avicennia tomentosa* und *Laguncularia racemosa*," *Flora*, 1889, p. 83.

*Laguncularia racemosa* have broadened the knowledge of these organs.

Before leaving this subject of transpiration, mention may be made here of some potometric measurements. At the Tortugas Laboratory a few potometer records were taken with shoots of *Rhizophora* to form some actual quantitative estimate of the water transpired through the leaves. Shoots of an average weight of 3.2 grams were used and the same conditions of humidity, light intensity and temperature were arranged as for the transpiration records above mentioned. It was learned that the average transpiration of these shoots was approximately one cubic centimeter in thirteen and four tenths minutes. This data, however, has no direct relation to the data of the bulk of the experiments performed.

## Biochemical Experiments and Tests.

As mentioned in the prefatory statement attached to this paper, certain biochemical investigations were carried on at the Tortugas Laboratory on the cellular contents of the *Rhizophora* seedlings, the two substances being dextrose and tannic acid. The purpose in undertaking the investigation was to gain some idea, if possible, of the rôle played by the tannin in the physiology of the mangrove, since this occurs in such large amounts in the plant's tissues. Several authors have suggested the various functions played by tannin in the plant's economy; Wiesner, for instance, believed that tannin is an intermediate product in the formation of resin, since it has been observed that in *Pinus,* as the tannin decreases in the spring, *i. e.,* during the season that the resin is most abundant, there is a corresponding increase in the resin. Basset[125] has suggested that the tannin content of fruits more particularly depends on certain enzymes. Buignet,[126] in his work on the banana, argues that from the diminution of starch and tannin as the truit ripens, there is ground for supposing that tannin assists in the formation of sugar. On the other hand, Gerber[127] in his studies on the relation of the

[125] Basset, B., Ref. Haas and Hill, 131.

[126] Buignet, A., *Ann. de chem. et de Phys.,* III., Ser. I., LXI., p. 281, 1861.

[127] Gerber, C., *Ann. de Sci. Nat.,* IV., 1897, pp. 1–280.

same substances in the ripening fruits of the Japanese persimmon considers the tannin decrease in the ripening process to be due entirely to the oxidation of tannin and that it does not at all contribute to the formation of carbohydrates. His reason for this conclusion is that in the conversion of tannin into carbohydrates more carbon dioxide would have to be liberated than oxygen absorbed, whereas in fruits the relation is the reverse.

Moore[128] contributes the idea that tannins may play an important part in the lignification of cell walls. Drabbel and Winterstein[129] make the suggestion that their rôle is important in cork formation, while Van Wisselingh[130] has given the latest suggestion in that they help materially in the formation of cellulose in some plants as *Spirogyra*. The bulk of facts known, however, about tannins do not lead one to suppose that they are used up in the plant generally since they are left in parts discarded by plants, as fallen leaves and not translocated, but even this does not assume much significance since sugar and starch, etc., are also often found in fallen leaves, and as Haas and Hill[131] remark, "A consideration of other facts does not tend to support the idea of tannin being of the nature of a reserve food." "Hillhouse,[132] for example, found that if a fuchsia having an abundant supply of tannin be grown in the dark there is no diminution in the substance in question."

Notwithstanding the conflicting opinions regarding tannin and the rôle it plays in the plant's physiology, it was decided to make a series of experiments on the tannin of the hypocotyl of young seedlings, since in these storage organs it occurs in such great abundance together with starch. With the hypothesis that perhaps the tannin of the hypocotyl is broken down to form sugar as the growth of the seedling proceeds, by the action of some enzyme as tannase, tests were made for such an enzyme and also on the relative reaction for dextrose and tannic acid. About ninety-five tests were

[128] Moore, A., *Journal Linn. Soc.*, London, Bot. 27, 1891, p. 527.

[129] Drabbel, A., and Winterstein, E., *Biochemical Journal*, 2, 1906, p. 96.

[130] Van Wisselingh, C., *Konen Akad van Wetensch. Amsterdam*, 1910, p. 685.

[131] Haas, P., and Hill, T. G., "Chemistry of Plant Products," London, 1913, p. 219.

[132] Hillhouse, B., *Midland Naturalist*, 1887–1888.

made by such methods as suggested by Abderhalden,[133] Euler,[134] and more particularly Thatcher,[135] who endeavored to isolate the enzyme, tannase, from several varieties of apples.

## Methods.

The fresh green hypocotyls were cut up and weighed in ten-gram portions, *i. e.,* ten grams from each hypocotyl. These portions were then ground to a consistency of coarse saw dust by pounding in a mortar with a little distilled water. Each portion was then digested with 50 c.c. distilled water in a beaker on a water bath at 40° C. for a half hour and the extract pressed out. The semi-dry mass that remained was then further digested with 50 c.c. of distilled water, the extract pressed out and added to the first extract. This extract of 10 Gm. of hypocotyl was then filtered and divided into two equal portions and each one made up to 100 c.c. by the addition of distilled water. One flask of the filtrate was boiled several minutes, then to each flask of filtrate a tenth gram of Merck's standard tannic acid was added and both placed in an incubator at 40° C. for twenty-four hours. After allowing this interval for the enzyme to effect a change in the tannin content in the unboiled flasks, both the control flasks and the unboiled ones were treated with four drops of concentrated ferric chloride to cause precipitation of the tannin and the characteristic change in color. In some of the tests the precipitate, bluish black in color, was filtered off and then carefully washed, desiccated and weighed, but in all these tests there was not any evidence to indicate the presence of the enzyme tannase in the hypocotyl of these plants. The color reactions for the boiled was just as dense as those for the unboiled portions, while the weight of the desiccated precipitates likewise showed no appreciable difference, so the absence of the enzyme is apparently substantiated.

Simultaneously with the performing of the above experiments a complementary series of investigations was made to show the

[133] Abderhalden, E., "Handbuch der Biochemischen Arbeitsmethoden," Berlin, 1910.

[134] Euler, Hans, "Allgemeine Chemie der Enzyme," Wiesbaden, 1910.

[135] Thatcher, R. W., "Enzymes of Apples," *Jour. Agri. Research,* 1910.

relation between the amounts of dextrose and tannic acid in the hypocotyls of different ages. A condensed report of this work was given in an earlier paper;[136] however, the methods, slightly more in detail, may be appropriately described here. The seedlings, as collected in the beds, were of assorted sizes, but all presumably of the crop of the spring or late winter months of the same year. These seedlings were carefully measured in regard to the length of the hypocotyl, stem, internodes, size of leaves, etc., and then assorted into groups of successively large growths. In making the extracts, ten grams of hypocotyl seedlings of uniform size were ground up in a morter with a little distilled water, just as in preparing the tannase tests. Some extracts were made by boiling and others by infusion, but no difference in strength was noted. After pressing through cheese cloth each extract was made up to the original fifty cubic centimeters with distilled water. The extracts at this stage were of a rather thick syrupy consistency and a clear orange red in color. To each fifty cubic centimeters then was added five c.c. of a saturated solution of lead acetate, a few drops at a time, this precipitated the coloring matters, phlobaphenes, etc., in the extracts and after standing four hours, each extract was filtered by means of a suction filter. The clear straw-colored filtrates were then treated with a steady stream of hydrogen sulphide gas for about ten minutes. This precipitated the lead as heavy black lead sulphide. After filtering off the lead sulphide and boiling to remove any $H_2S$ remaining in the extracts, the filtrates were tested, one drop of cresol being added to each extract to prevent the growth of moulds.

As quantitive analyses were not feasible at Tortugas, colorimetric methods of testing were resorted to. For the testing for dextrose, Huizinga's Test was used. This is a reduction test, which was found to work very well with the *Rhizophora* extracts. One c.c. of the extract was pipetted into each of a series of test tubes and diluted with five c.c. of distilled water, then one c.c. of 0.1 KOH solution was added and one c.c. of a saturated solution of ammonium molybdate was pipetted also into each tube. The tubes were then boiled over an alcohol flame for 1.5 minutes and then to

136 Bowman, H. H. M., Report on Botanical Investigation at Tortugas Laboratory, Season 1916, *Carnegie Inst. of Wash. Year Book*, No. 15, p. 188.

each one was quickly added ten drops of concentrated HCl. A deep blue color, in varying degrees of intensity dependent on the amount present, indicated the dextrose.

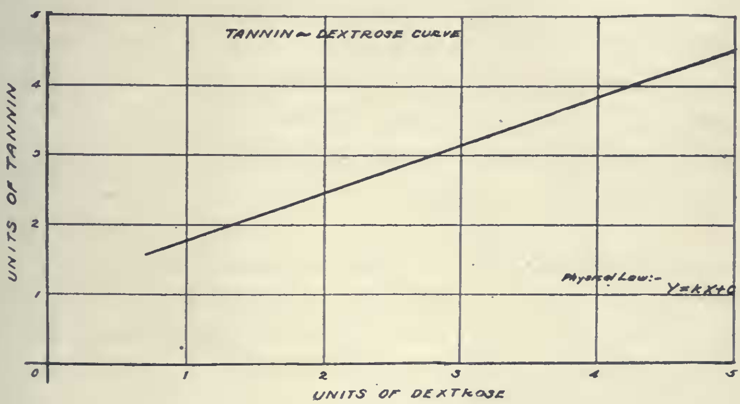
The tannin was tested for by means of Hager's Test, after experimenting with various tests, as Gayard's, Grigg's, Oliver's, Vogel's, Watson's and Young's, the one selected was found to be the best for the material in hand, just as Huizinga's Test for Dextrose seemed to be the best of nine other tests tried. The test for tannin consisted in placing one c.c. in each of a series of test tubes and diluted with five c.c. of distilled water. To each was then added one c.c. of a saturated solution of hydrogen sodium phosphate ($Na_2HPO_4$) and a single drop of rather strong ferric chloride solution, when a precipitate of a bluish violet color occurred in proportion to the amount of tannin present in the tubes.

Why these tests and reagents seemed to be the best for testing the substances in question in the mangrove extracts is not known, but it probably depends on the peculiar composition of *Rhizophora* tannin, etc. The tannin of the red mangrove, according to the classification of Haas and Hill, belongs to the Pyrocatechol Group, but as these authors state on account of the incomplete status of knowledge regarding the tannins as a whole and of the chemistry of this group in particular, it is a very difficult matter to classify them properly. According to Kraemer[137] the tannins of the above group produce protocatechuic acid on fusion with potassium hydroxide and phlobaphenes on treatment with acids. A very careful analysis of the bark extract of *Rhizophora* was made by Trimble.[138] His results showed that no gallic acid was present and that in the dry total tannic acid occurred to the amount of 23.92 per cent. and mucilage 1.72 per cent., glucose .81 per cent., albuminoids 7.02 per cent., starch 4.27 per cent. and cellulose 27.49 per cent. Although perhaps the reagents were adapted to this group of pyrocatechol tannins, the results of the tests signify merely a relative value, for the quantities of the substances in question. Thus the comparison colorimetrically of the individual tests of each plant with that of a

[137] Kraemer, H., "Applied and Economic Botany," Philadelphia, 1914, p. 204.

[138] Trimble, H., "Mangrove Tannin," *Univ. of Penna. Bot. Lab. Contributions*, Vol. 1, No. 1, 1892, p. 50.

tube of standard dextrose solution of known strength is the basis of these records. The standards are in five grades, each being a certain definite percentages of Merck's standard tannic acid, or Kahlbaum's standard dextrose. The amounts by this comparative method of testing were placed in the five arbitrary units, approximating the same color as that for 0.5 per cent. standard dextrose solution on the one hand, and a 0.125 per cent. standard tannic acid solution on the other, with successive dilutions by half of these standard solutions.




Graph No. 3.

The tests were made in series of twelve, that is a dozen seedlings of progressive increase in size were selected from which to make extracts at one time. More could not be handled conveniently at one time, since the length of time required to carry the extracts through the various precipitations, filtrations, etc., gave opportunity for mould spores to germinate in the flasks, a difficulty very hard to control in a warm, moist climate. About two hundred of these tests were made and the various series of twelve seedling-extracts were averaged to obviate errors in judgment regarding color intensity, etc. Graph No. 3 illustrates the relation of the two substances in question as they occurred in seedlings of progressively larger growth according to the above tests. The ratio may also be expressed by the equation $y = Kx + C$, where $C$ approximates 1.05 and $K = 2/3$, the ordinates, $Y$, express units of tannin and the abscissæ, $X$, units of dextrose. By this graph then it is seen that the unit increases in tannin for plants of progressively larger growth vary as ⅔ of the unit increases in dextrose, *i. e.*, the ratio is constant and the "curve" is really a straight line.

The result is rather contrary to the writer's expectations, since on account of the extraordinary amount of tannin in the hypocotyl, an agreement with the "reserve food" theory, as put forth by Buignet, etc., *i. e.*, the two substances in inverse ratio, was looked for. The results, however, conform to the opposite view as expressed by Gerber, that is that tannin does not play a definite part in the direct nutrition of the mangrove seedling.

Before leaving the subject of tannins and physiology in general it is interesting to note that in Reed's experiments,[139] tannic acid and pyrogallol when added to cultures of wheat seedlings produced large increases in transpiration. Warming[140] regards tannin as of some importance in water conduction and in another place says it functions especially as a protection against undue evaporation from plants during winter, and also suggests that it may be a means of rapidly restoring turgor. Regarding the function of tannin in the leaves of *Rhizophora*, the view is here expressed for the first time, so far as the writer knows, that the two layers of tannin cells in the water hypodermis serve as an insulation against light and heat and a protection to the water storage cells beneath it. Schimper[141] has shown that the strand plants need shade and cloudy skies for their best development, since the direct sunlight heats up the interior of the leaves and the increased transpiration thus brought to a very high degree is injurious to the plants. In conclusion it is here stated then that the tannin in the leaves acts as an additional protection against transpiration, and also that the tannin of the hypocotyl does not contribute directly to the nourishment of the seedling.

## Ecology.

Practical work on the ecology of the mangrove in southern Florida was suggested by the work of Praeger[142] as published in the

[139] Reed, H. S., loc. cit., p. 107.

[140] Warming, Eug., loc. cit., p. 539.

[141] Schimper, A. F. W., "Plant Geography," 1903, p. 404.

[142] Praeger, R. L., "Buoyancy of Seeds," *Proc. Scient. Royal Dublin Soc.*, rev. by E. W. Berry, *Plant World*, Vol. 17, No. 4, p. 131.

Scientific Proceedings of the Royal Dublin Society and reviewed for *Plant-World* by E. W. Berry. This work deals exhaustively with the buoyancy of seeds and his observations on seeds of over 900 British plants show that the more buoyant forms are inhabitants of streams, banks or seashores. The results showed that 85 per cent. sunk at once or within a week, 5 per cent. floated 1 to 4 weeks, 33 per cent. 1 to 6 weeks, 1.9 per cent. 6 to 12 months and 4.4 per cent. floated over 12 months. In consideration of these results and as the life and dissemination particularly of the viviparous seedlings is dependent on buoyancy it seemed worth while to undertake some investigation of this and related phenomena concerned with dissemination. Guppy has done such excellent work and made such complete observation on the buoyancy of the mangrove seedlings that no work on buoyancy was required, that writer's latest book[143] giving a summary of observations along this line. Harshberger's works[144–145] on the ecology of South Florida also were of a simulating effect and a helpful reference in the present work on the mangrove of the region, as well as Webber's notes[146] and the journals of the Agassizes.[147–148]

The relations of these mangroves to their environment have been a subject of much interest to ecologists and botanists in general from Theophrastus to the present, and many philosophical discussions have been given concerning their origin and adaptation to their habitats. In these adaptations, however, they only perhaps show in more marked degree what all plants of strand floras show, viz., strongly developed xerophytic characters, in spite of the fact that the environment is aquatic. These characters have been fully discussed by such writers as Holtermann[149] on the effect of climate

143 Guppy, H. B., loc. cit., p. 109.

144 Harshberger, J. W., "Vegetation of South Florida," *Trans. Wagner Inst. of Sci.*, VII., 3, 1914, pp. 74–80.

145 Harshberger, J. W., "Phytogeography of North America."

146 Webber, J. H., "Strandflora of Florida," *Science* (N. S.), VIII., 1898, p. 658.

147 Agassiz, Louis, "Florida Reefs."

148 Agassiz, Alexander, "Three Cruises of the *Blake*."

149 Holterman, Carl, "Der Einfluss des Klimas auf den Bau der Pflanzengewebe," Leipzig, 1907.

on plant tissues, and Warming,[150] Haberlandt,[151] Karsten and others who have all emphasized some special features of this ecologic relation.

The general impression of a mangrove swamp is very aptly described by Warming (*loc. cit.*): "The bottoms of the crowns of the trees are usually truncate and stand a small distance above the water, and beneath them are seen, where *Rhizophora*-vegetation forms the outermost fringe of vegetation, a tangle of countless brown roots more or less clothed with algæ. The soil, which in places is not covered with water at low tide, is soft, deep black mud, full of rotting, stinking organic bodies in which bacteria abound. The water between the trees may be covered with dirty film and bubbles of gas rising from the bottom burst at the surface." One may also add that the air is usually thickly filled with voracious mosquitoes.

In spite of this rather unpleasant, but truthful description, the mangrove formation holds a great many features of interest for the ecologist, as Karsten[152] says in describing the mangrove swamps of the Malay Archipelago—"Es ist ein Vegetationsbild von seltener Einförmigheit besonders für an tropischen Formenreichtum gewöhnte Augen und doch giebt es wohl wenige Gebiete, die bei näherer Bekanntschaft eine solche Fülle von interessanten Formen und Beziehungen zeigen." This uniformity to which Karsten refers in the oriental mangrove consists of nine widely diverse families, representing twenty-one species. Our American mangrove swamps, however, are much more "uniform" than this. Harshberger has summarized the species in the various kinds of mangrove thickets (*loc. cit.*, 144, p. 77) as they occur on the Peninsula of Florida for the most part with brief notes on the vegetation of the Keys. The whole aggregation of species which grow in all the types of mangrove formations, whether it be along the rivers, bays or open sea, on islands or everglades, embrace about twenty-eight species, including pteridophytes, floating aquatic plants, epiphytic lichens, etc. The trees of the typical mangrove habit, that is, those plants which

[150] Warming, Eug., "Œcology of Plants," tr. Vahl, Groom and Balfour, Oxford, 1909, p. 234.

[151] Haberlandt, G., "Eine Botanische Tropenreise," 1893, p. 182.

[152] Karsten, G., loc. cit., p. 3.

by their structural adaptations and, particularly, vivipary, constitute "the mangrove" in the sense of the French and German botanists, only comprise in the American mangrove thickets of Florida, four species. These are the red mangrove, *Rhizophora mangle* L., the black mangrove, *Avicennia nitida* Jacq., the white buttonwood, *Conocarpus erectus* Jacq., and *Laguncularia racemosa* Gärtn. This last species is not contained in Harshberger's lists and perhaps was not seen by him, although it occurs quite abundantly in the keys, particularly the more southern ones. Dietrich Brandis, writing on its range in Engler and Prantl, says, however, that on approaching its northern limit it becomes merely a low shrub, and hence easily overlooked. At Ragged Keys, for instance, trees were observed three to four meters tall growing on the outer edge of the fringe vegetation associated with *Rhizophora*. *Laguncularia* grows in fairly deep water along shore with the red mangrove, while *Conocarpus* and *Avicennia* are, for the most part, in shore on ground that is only submerged at high tide, or not reached by the daily tides at all. On approaching a mangrove island or shore this feature is easily seen, the rich olive or bright green of the two species growing in deeper water is noticed as a dense wall about two meters tall with a line of brown along the water's surface which is composed of the tangle of aërating prop roots of *Rhizophora,* and the small knotty pneumatophores of *Laguncularia*. In the background, stretching above these two outer species, appears the silvery white and light green of the *Avicennia* and the *Conocarpus*. At some places, however, *Avicennia* grows out in fairly deep water and produces its large area of apogeotropic slender yellowish-brown aërating roots also.

## Physiological Considerations of the Ecology.

The adaptations of mangroves to their environment have been grouped by Warming (*l. c.*, p. 236)[150] under several heads as fixation, respiratory roots, germination and vivipary, means of migration, and xerophytic structures. This last heading is best illustrated in the leaves, as being perhaps the most plastic organ and hence most easily adaptable. The structure of the leaves of *Rhizo-*

*phora* has been described in detail in the chapter on morphology, but several studies were made on the leaves to learn to what extent the adaptation is carried in different habitats, or rather media of growth. To this end then, leaves were secured from trees growing in fresh water along the Miami River, from trees growing in pure salt water off shore in the Atlantic, northeast of Miami, and also from trees growing in the rather dry situations in the Marquesas atoll in the Gulf of Mexico, in soil only reached by the highest tides and in the same atoll, of trees growing off shore in salt water several feet deep. Sections were made of these leaves in various preparations, free hand, of fresh and pickled material, and also paraffine preparations, and comparisons made of the thicknesses of the leaves and the relative amounts and positions of the various tissues in the leaf. Drawings and microphotographs were made and are here given. In each of the two sets of preparations leaves were selected of the same dimensions and at about the same node back from the bud so that the compared leaves were as nearly alike as could be possible. As a rule, however, the leaves on trees in fresh water were slightly larger than those for the corresponding node in salt water trees. In Fig. 2, Pl. VII., is seen the illustration of the fresh water section. It will be noticed that the tannin cells of the hypodermis are shorter and rounder, the water storage cells are smaller and only in two rows, the palisade is thicker and the spongy parenchym not so deep and the stomata slightly larger than the corresponding features in the salt-water leaf section shown in Fig. 1, Pl. VII. The greatest difference seems to be in the amount of water storage tissue and the lengths of the palisade cells. In the salt-water leaf the palisade lies almost in the middle of the leaf, and the tannin cells are also rather larger and elongated; this detail also helps to strengthen the writer's view regarding the function of these layers of cells as insulation against the heat and light. The ranker growth of the river bank mixed with other trees help to make more shade for the trees in this situation. The sections of the inshore leaves, and the offshore leaves show much the same relation on a comparison of the sections, but in a less striking degree. The offshore leaf (Fig. 4, Pl. VII.) is the thicker, *i. e.*, showing a typical halophytic reaction, while the inshore leaf (Fig. 3, Pl. VII.) is slightly thinner.

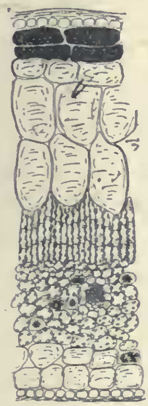


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FIG. 1. Transverse section leaf from salt-water grown tree, showing distribution and relative quantities of the leaf tissues. (Cam. luc.) × 133. Dark cells containing tannin, clear cells water storage hypodermis. Columnar cells of palisade, and beneath them spongy parenchyma containing crystals and section of vascular bundle. Below a loose hypodermis.

FIG. 2. Transverse section of leaf from tree growing in fresh water. Regions same as Fig. 1. (Cam. luc.) × 133.

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FIG. 3. Transverse section leaf from tree grown in shore. Regions same as Fig. 1. (Cam. luc.) × 133.

FIG. 4. Transverse section leaf from tree growing off shore. Regions same as Fig. 1. (Cam. luc.) × 133.

The difference in palisade and tannin cells is not so pronounced here as in the preceding set of comparisons, the main difference being in the amount of water storage tissue. On account of the slight quantity of rain water held in the soil, or of the chemical action of the soil producing a lessening in concentration of the salt water as it seeps inshore, the inshore leaves are thinner and show the tendency toward adaptation, as seen in the fresh-water leaves.

It might be mentioned in connection with these preparations that the drawings were made by means of a *camera lucida* and that the actual leaf thicknesses were as follows: Fresh-water leaf, .54 mm., salt-water leaf, .65 mm., inshore leaf, .42 mm., offshore leaf, .54 mm. The first pair of comparisons must not be based with the measurements of the second pair, as the material was collected at different times of the year, different regions and were perhaps different in leaf size or age.

## Vivipary and Dispersal.

Perhaps the most peculiar of all the adaptations of mangrove-habit plants is that of vivipary, and this seems to be best developed in members of the Rhizophoraceæ that grow in the deepest water and softest mud. This adaptation has a very vital ecological significance in connection with dispersal, as remarked at the beginning of this chapter concerning Praeger's experiments, and the more recently published results of Guppy. Vivipary, according to Goebel's[153] view, is only found in plants which grow under very warm, moist conditions and this wet environment which quickly germinates seeds has produced the habit, that is the habit arose by the differences in the readiness to germinate in various seeds.

The first sign of vivipary then would be the falling to the ground of an immature seed, with the embryo still undeveloped, a condition somewhat analogous with that of the seeds of certain orchids; next would be the stage when the seeds germinate as soon as shed on the ground; third is a type represented by *Laguncularia* in which the seedling just begins to germinate on the tree, then fourth, where germination is completed on the tree, but the seedling immediately falls as in *Avicennia* and the climax is reached in

[153] Goebel, K., loc. cit., p. 123.

*Rhizophora,* where the germinated seedling stays on the parent tree for nearly a year. Guppy[154] has put forth the unique view that in a previous early geological age, under uniform warm, moist climatic conditions and a very diffuse light due to constant cloudiness, the viviparous habit was universal and that vivipary and the conditions of the present mangrove swamp are an index both to the meteorological conditions and to the forms of a very ancient vegetation. The seedlings, being viviparous then, by evolution through one of these processes presumably, although the writer rather inclines to the former conclusion that the habit arose by small beginnings, the dispersal of these depends on the ocean into which they fall.

The dispersal of the mangrove seedling has been discussed very fully by several authors, at greatest length perhaps by Guppy, as observed in the Fiji Islands and the Pacific, and more latterly in the middle Atlantic coasts. This author regards the currents as the source of dispersal, since in quiet water the seedling may drift for months, but when they are buffeted by each other or floating objects for any length of time, the plumule is injured and the seedling dies. The present writer, nevertheless, has found many drifted seedlings in the Tortugas which had been broken either at the plumule end or the radicular end and in spite of these mutilations put forth adventitious buds at the lenticels at one end, or roots at the lenticels near the radicular region. The nearest mangrove trees in this case were those of the Marquesas atoll at a distance of twenty-five miles from the Tortugas group. Intimately associated with the buoyancy of the seedlings is their position in the water. Guppy noted that they float vertically in fresh water and horizontally in salt water, while they incline at various angles in dilutions of various densities. A fortuitous agreement is seen in this relation between the specific gravity of the seedling and the density of the water, for the horizontal position keeps the plumule moist and uninjured by the fierce sunlight. The seedlings have no buoyancy until the hypocotyl has emerged from the fruit about six inches in the case of *R. mucronata* and the same has been observed by the writer for young seedlings

[154] Guppy, H. B., "Observations of a Naturalist in the Pacific," Vol. II., Plant Dispersal, 1906, p. 470.

of *R. mangle*. Guppy estimates that 95 per cent. of seedlings that fall into the sea do float, and has further carried out a most interesting series of experiments in England with seedlings brought from the tropics and kept dry for five months. These experiments, which show the prolonged vitality of the seedlings, recall the words of Plutarch quoted in the first chapter of this paper, where he described the "anacampserotes" as being plucked out of the sea and hung up to dry, and which bud and put out green leaves presumably when placed again in water.

The manner in which seedlings come to take roots after having journeyed for weeks in the ocean currents is also of interest to an ecologist, because it is only on certain shores that the seedlings really can eventually form a mangrove swamp. In the Tortugas and other similar shores with wide beaches of coarse sand the essential conditions are lacking and the seedlings go through a short life cycle which the writer has reproduced under similar conditions at the laboratory and always with the same result. The plants are dropped from the trees in February, March and April in greatest number in the thickets of the Marquesas, Boca Grande, or islands even further east, these drift twenty-five to seventy-five miles westward with the counter Florida current and the high spring tides carry them up on the higher beach terraces formed in the coarse shifting sand of the Tortugas with masses of *Sargassum* and the broken leaves and rhizomes of *Thalassia* and *Cymodocea* which form long windrows on the beaches. If there is sufficient of this debris to conserve moisture during the dry summer months when it acts as sort of a mulch for the *Rhizophora* seedlings, the little plants grow and the plumule lengthens and forms several rather short internodes. These may last with a desultory growth into late summer and perhaps be all swept away from their bed in the shifting sands by the autumn storms and hurricanes. As a rule, however, the seedlings are buried more or less deeply in the sand with not sufficient debris, since this flotsam is lighter and is flung a little farther back on the beach than the seedlings are. During the summer the plumule expands and the leaves put out, but these leaves never get over two centimeters long and are soon burned up by the intense heat and light of the glaring white beach and killed by the drying wind.

These leaves are put out successively with very short internodes until the reserve food in the hypocotyl is exhausted and the seedling dies. The same sequence of events happened in the laboratory cultures described in a previous chapter in which some young seedlings were set out in boxes of sand about fourteen inches deep and watered daily with sea water. The plants eventually died through the exhaustion of reserve food and an inability to compensate the loss in food by the activities of new synthetic tissues. The plants were kept in full sunlight in coarse sand and merely watered with salt water, the amount in excess of that held in suspension in the soil flowing out of the box below.

Mangrove seedlings have an equally hard time in getting a foothold on rocky shores as described by Crossland.[155] He observed that the hard coral rock of the Zanzibar Reef formed a plane floor with very little mud and many small cracks, but was puzzled to see how the *Rhizophora* became planted in such small holes. While Crossland does not mention the density of the water, it seems that the water along these reefs must have been largely diluted with fresh water since he remarks that the seedlings floated vertically. By close observation, he noticed that the eddy and current gave a twirling motion to the seedling, which in turn produced a boring action on the shallow bottom until the radicle became lodged in a little crack. Success for anchoring on these reefs depended on quiet water and gentle ripples and suitable crevices on the bottom.

In connection with the dispersal and anchorage of seedlings, a number of observations were made on the character of the bottom, the depths of the water, etc., on the shores of Key West, Stock Island and other adjacent keys (Fig. 4, Pl. VIII.). Key West being composed of hard oölithic rock and mud flats of hard precipitated mud, the conditions observed by Crossland at Zanzibar are duplicated at some places and seedlings which take hold in the crevices of this hard oölite cannot be pulled up, but the root will break off, owing to the tenacious hold in the cleft. On these flats both *Avicennia* and *Rhizophora* seedlings were observed starting growth in 8–37 centimeters of water at high tide. On Stock Island the same conditions

[155] Crossland, C., "Note on Dispersal of Mangrove Seedlings," *Annals of Botany*, XVII., p. 267.

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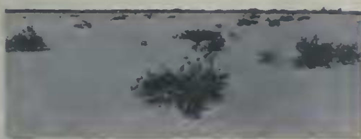

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FIG. 1. Stunted mangroves on sand flats in Andros in the Bahamas. Photo. by Small.

FIG. 2. Hurricane damaged swamp at Boca Grande.

FIG. 3. *Tillandsias* epiphytic on red mangrove in the Bahamas. Photo. by Small.

FIG. 4. *Rhizophora* on hard oölite flats on Stock Island at low tide.

FIG. 5. Mangroves growing in dry coral sand some distance in shore at Boca Chica.

FIG. 6. *Rhizophora* tree with roots dug out to show absorptive system and props, Mangrove Island near Key West.

obtain as Key West, measurements here of trees which were representative of all the trees about the lower Florida Keys showed the average tree to be 3–4 meters, growing on oölite with only 2–5 centimeters of mud covering the absorptive roots (Fig. 6, Pl. VIII.). These absorptive roots were 20–40 centimeters long and 1–2 centimeters in diameter, while the prop to which they were attached was of an average length of 1.8 meters, the shoot of the props being about 1.5–2 meters. The hydrometer seedlings for the water here, on June 25, was sp. gr. 1.0205 at 34° C. On June 5, at the same place where seedlings were grown off shore in 20 cm. of water, the seedlings were almost similar; T. 34° C. and sp. gr. 1.021.

At Boca Chica, the conditions were slightly different, the observations made on June 9 at low tide. The trees were growing in deep mud almost a meter deep and were about five meters tall, the roots being covered, at low tide, with 10–20 cm. of water. Hydrometer seedlings here showed a sp. gr. of 1.0235 at 30° C. On this island also were seen *Rhizophora* trees growing five to eight meters in shore in apparently dry shell sand, in a healthy condition (Fig. 5, Pl. VIII.).

At Cayo Agua on June 17 and 24 about the same measurements were made as at Boca Chica, except that here trees were found full of flowers and fruits at all stages as well as pendant seedlings. At no other island in the lower keys were flowers noted at this time of the year. On the west side of the island a hurricane of a previous winter had broken and washed up a considerable area of the swamp, and in this close mass of dead and white bleached twigs and branches, the ideal situation seemed to be afforded to the young seedlings to start growth. The dead twigs overhead provided a lattice of the right sort for optimum light intensity, while the decaying branches in the mud below offered quiet water and debris for anchorage. The same thing was seen in the hurricane damaged swamp at Marquesas (Fig. 2, Pl. VIII.).

At Mangrove Island, Crawfish Key and Ragged Keys trees five to six meters high were observed growing in deep mud. At the last mentioned keys the mangroves were associated with *Avicennia*, *Conocarpus* and *Laguncularia*. At Bahia Honda and Duck Island only the inner or Gulf side of the islands have a mangrove fringe on account of the sandy beaches on the outer shore. In rich alluvial soil of the river hammock along the Miami River, the *Rhizophora* and other trees form a jungle seven to eight meters tall, while back in the Everglades, *Rhizophora* only in the form of small bushes were observed scattered in the saw grass, *Mariscus jamaicense* (Crantz) Britton. This has also been observed by Harshberger (144, *loc. cit.*) and Dr. J. K. Small[156] who has published voluminous reports and floras of the region, and has kindly furnished some photographs, illustrating this peculiar condition of the mangrove here and on Andros Island in the Bahamas (Fig. 1, Pl. VIII.). This island is interesting to us because it is the place that Catesby described in his early chronicle. At Boca Grande, *Rhizophora* seedlings were observed starting to fill in a thickly vegetated salt meadow, which became flooded at high tide; this marsh was covered largely with *Batis maritima, Sesuvium portulacastrum, Borrichia,* etc., and among them were many thrifty young *Rhizophora* seedlings. It is supposed that these seedlings were carried into this meadow by unusually high tides.

## Experimental Data.

Harshberger's experiments (*loc. cit.,* 144, p. 79) suggested a line of work on the station of *Rhizophora* in estuaries which have been carried out in Biscayne Bay and the Miami River. Since these experimeters have been made by the writer, Guppy's book (*loc. cit.,* 143) has appeared and this naturalist also has made some study of this subject in Fiji and Ecuador. In Fiji, Guppy found that where both *R. mucronata* and *R. mangle* grew luxuriantly on the coast the latter followed up the estuaries and river banks. Despite the fact then that *R. mangle* is a salt swamp plant it apparently can adapt itself to practically fresh-water conditions as the transpiration cultures in this work show for individual cases. Dr. Small also has told the writer that he has observed in the Everglades and the Bahamas *Rhizophora* growing, by the square mile area, miles from any salt water. In the face of these cultural experiments on a small laboratory scale and the observations of Small, the evidence afforded

[156] Small, J. K., "Exploration in the Everglades and on the Florida Keys," *Jour. N. Y. Bot. Garden,* 15, 1914, 69–79.

by the writer's own ecological notes along the Miami River, and Guppy's observations in the Black River, Jamaica, show the fact to remain that salt water is needed for the proper development of a typical mangrove vegetation. The trees observed in the Everglades and on other places in the interior of swamps having a fresh-water substratum are of small size and poorly developed.

To account for their origin and growth, even though poor, in such interior swamps, it is logical to suppose that they have been carried thither by currents flowing into the estuaries from the sea, and for their continued existence we may suppose that the soil is still sufficiently salt from previous inundations, or that the currents which carry the seedlings in are slightly brackish and so impregnate the soil with a little salt. It is regretable that no data are available on the salinity of the soils of such interior swamps where mangroves are growing in this stunted condition.

To return to the experiments made by the writer in the Miami River and Biscayne Bay, it has been long known that in certain estuaries there is an up-stream current of salt water which flows on the bottom, while a down-stream current of fresh water flows on the surface. In earlier observations along the Miami River, Arch Creek, etc., the writer noted the gradual decrease in stature and frequency of occurrence of mangroves as the river was ascended until after three or four miles they had disappeared entirely. It was supposed that this feature, which has often been remarked by other ecologists, was in some way connected with the salinity of the water, accordingly it was determined to make some top and bottom hydrometer readings. To do this the launch *Darwin* was employed and the deep-sea water-sampling instrument taken from the equipment of the institution's yacht, *Anton Dohrn*. This instrument is a very ingenious device designed by Dr. Mayer and the late Mr. Drew in the latter's work with bacteria in the sea water of the Tortugas region. The instrument consists of a glass cylinder enclosed in a heavy brass jacket. The top and bottom of the cylinder are closed by means of brass plates, which fit tightly and are operated by strong springs. The instrument is lowered into the sea and on the yacht it is attached to the sounding machine and lowered mechanically, and if samples are taken from deep sea water the instrument is filled with alcohol. When the bottom or any desired depth is reached a heavy weight is sent down the slender wire cable which attaches the instrument to the boat. This weight operates a clip which releases the spring and the alcohol is allowed to escape and the sea water flows in, another weight is sent down which falls on a different clip and the instrument is closed, and the sample drawn up in a few seconds. In these experiments, alcohol was not needed; as the depths in the river at no place exceeded nine feet, and as the launch was used in place of the yacht, the instrument was lowered by hand instead of the sounding machine. Samples were taken then from both the top and the bottom layers and hydrometer readings made of them. The readings were begun at 9.15 A.M. on the outer side of the harbor, in the Atlantic, one quarter mile off shore, the second made just off shore near the mangroves growing on the outer side of the Harbor near the Government Channel. Then another halfway across the Bay (Bay Biscayne) and the next at the mouth of the Miami River, from thence every half mile up stream until *Rhizophora* no longer appeared. These readings are tabulated below.

By these readings it is seen that there is a very decided difference in the salinity of the top and bottom layers. The distribution of the mangroves is also correlated with the comparison of the top and bottom readings and we may infer that the salt of the water which is carried up by the under-current is the factor in the physiological relations of the plant which compose the optimum conditions for its growth and as this decreases in concentration by dilution with the downstream current, the *Rhizophora* fringe gradually dwindles and disappears.

### Dimorphism.

Before leaving this chapter on ecology, a word may be said regarding dimorphism in the genus, *Rhizophora*. Guppy has recorded very obvious dimorphism in *R. mucronata* in Fiji and in *R. mangle* in Ecuador, the double form in the first consisting of a fertile type and a sterile (selala) type in which the pollen is not viable. The second species consists in Ecuador of the "mangle grande" and the "mangle chico," a tall and a little mangrove. The